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An Assessment of the Feeding Habits of Harbour Seals *(Phoca vitulina)* in the Strait of Georgia, British Columbia, Based on Scat Analysis

Peter F. Olesiuk, Michael A. Bigg, Graeme M. Ellis,
Susan J. Crockford and Rebecca J. Wigen

Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6

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AN ASSESSMENT OF THE FEEDING HABITS OF HARBOUR SEALS (*Phoca vitulina*) IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA, BASED ON SCAT ANALYSIS

by

Peter F. Olesiuk[1], Michael A. Bigg[1], Graeme M. Ellis[1],

Susan J. Crockford[2] and Rebecca J. Wigen[2]

[1]Department of Fisheries and Oceans

Biological Sciences Branch

Pacific Biological Station

Nanaimo, British Columbia V9R 5K6

[2]Pacific Identifications
4053 Nelthorpe Avenue
Victoria, British Columbia V8X 2A2

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TABLE OF CONTENTS

ABSTRACT v
1. INTRODUCTION 1
2. SAMPLE COLLECTION AND ANALYSIS 3
2.1 Scat collections 3
2.2 Processing of samples 4
2.3 Sample interpretation 5
3. DATA ANALYSIS 6
3.1 Relative importance of prey 6
3.2 Seasonal and regional variations in diet 8
3.3 Absolute importance of prey species 9
4. PREY SPECIES 12
4.1 Scat contents 12
4.2 Precision of identifications 13
Gadidae 13
Clupeidae 13
Salmonidae 14
Batrachoididae 14
Embiotocidae 14
Cottidae 15
Pleuronectidae (and possibly Bothidae) 15
Hexagrammidae 15
Scorpaenidae 15
Ammodytidae 15
Osmeridae 15
Other fishes 15
Unidentified fishes 15
4.3 Structures used in identifications 16
5. DIET COMPOSITION 18
5.1 Validity of assumptions 18
5.2 Diet within estuaries (Strait of Georgia) 23
Comox Harbour 24
Mud-Fanny-Deep Bays 25
Nanaimo River 25
Shoal Islets 26
Cowichan Bay 26
Mill Bay 27
Squamish River 27
Port Moody 28
Boundary Bay - Fraser River 28
5.3 Diet outside estuaries (Strait of Georgia) 29
Northern Gulf 29
Gulf Islands 30
Southern Gulf 31
5.4 Diet in other regions 32
Masset Inlet 32
Western Vancouver Island 32
Johnstone Strait 33

6. PREY CONSUMPTION 33
6.1 Annual food requirements 33
6.2 Annual prey consumption 34
6.3 Significance and patterns of seal predation 36
Gadoids 36
Pacific herring 37
Salmonids 39
Plainfin midshipman 42
Lingcod 42
7. DISCUSSION 43
ACKNOWLEDGEMENTS 48
LITERATURE CITED 49
TABLES 56
FIGURES 65
APPENDIX I 125
APPENDIX II 129
APPENDIX III 133

ABSTRACT

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730: 135 p.

Seasonal and regional variations in the diet of harbour seals in the Strait of Georgia were described based on 2,841 scat samples collected from 58 sites (11 estuaries and 47 non-estuary haulouts) in all months, and the diet compared with the diet in other regions of the province based on 159 samples. Prey remnants were separated from other faecal matter using an elutriator and prey identified using a wide variety of structures including otoliths, teeth, vertebrae, cranial, appendicular and caudal elements, and scutes and spines. Otoliths alone provided an incomplete and biased representation of the diet. We derived and employed a new index, referred to as split-sample frequency of occurrence, to assess the relative importance of prey. The validity of the assumptions underlying the index, and scat analyses in general, were addressed. Annual prey consumption was estimated by combining dietary information with data on the abundance and distribution of seals and estimates of their daily food requirements.

The diet in the Strait of Georgia was dominated by Pacific hake and herring, which comprised 42.6 and 32.4% of the overall diet respectively. The former was consumed primarily during April-November, which coincided with the post-spawning dispersal and movement of hake to shallower water, and the latter mainly during December-March, which coincided with the pre-spawning emigration of herring into the Strait of Georgia. Annual hake consumption in 1988 was estimated at 4,214 tonnes, which represented 3.5% of the total stock biomass or 71% of mean recent commercial harvests. Annual herring consumption was estimated at 3,206 tonnes, which represented 3.2% of the total stock biomass or 27% of mean recent commercial harvests. Salmonids comprised 4.0% of the overall diet and consisted mainly of adult salmon that were taken as they returned to rivers to spawn, especially in estuaries. However, predation on trout also appeared to have been significant in localized areas. Annual salmonid consumption was estimated at 394 tonnes, which represented approximately 2.8% of mean recent annual escapement. Lingcod comprised 3.0% of the overall diet and were preyed upon mainly during November-April when males were defending nests. Annual lingcod consumption was estimated at 294 tonnes, which was roughly equivalent to the recent commercial and sport harvests combined. Other important prey in the Strait of Georgia were plainfin midshipman (3.4% of overall diet), surf-perches (2.3%), cephalopods (2.1%), flatfishes (1.2%), sculpins (1.2%) and rockfishes (1.1%). The Strait of Georgia data, and the limited data collected from other regions, indicate the harbour seal is an opportunistic predator in that diets varied regionally and seasonally depending on the local availability of prey.

RÉSUMÉ

Olesiuk, P. F., M. A. Bigg, G. M. Ellis, S. J. Crockford et R. J. Wigen. 1990. Evaluation des habitudes des veaux marins (*Phoca vitulina*) en matière d'alimentation dans le détroit de Géorgie (Colombie-Britannique), à partir de l'analyse des excréments. Can. Tech. Rep. Fish. Aquat. Sci. 1730: 135 p.

Les variations régionales et saisonnières du régime alimentaire des veaux marins du détroit de Géorgie sont décrites à partir de 2 841 échantillons d'excréments recueillis à 58 endroits (11 échoueries estuariennes et 47 autres échoueries) pour tous les mois concernés. On a aussi comparé leur régime alimentaire à celui observé dans d'autres régiois de la province, d'après les résultats de 159 échantillons prélevés. On a séparé les restes des proies des matières fécales à l'aide d'un élutriomètre; on a identifié les proies grâce à des structures très variées, notamment des otolithes, des dents, des vertèbres, des fragments de crânes, d'appendices et de nageoires caudales, des acutelles et des épines. Les otolithes seules fournissent un tableau incomplet et faussé de l'alimentation des veaux marins. On a établi et employé un nouvel indice, appelé fréquence relative à l'échantillonnage fractionné, pour évaluer l'importance relative des proies. On s'est penché sur la valeur des hypothèses à la base de l'indice et sur les analyses des excréments en général. On a évalué la consommation annuelle de proies en combinant les données sur le régime alimentaire, les données sur l'abondance et la distribution des veaux marins, ainsi que celles sur les données estimatives des besoins alimentaires quotidiens des veaux marins.

L'alimentation des veaux marins du détroit de Géorgie est surtout composée de merlus et de harengs du Pacifique, qui constitutent respectivement 42,6 et 32,4 du régime alimentaire global. Le merlu du Pacifique a été consommé surtout d'avril à novembre, période qui coïncide avec la dispersion de l'après-frayage et le déplacement du merlu vers des eaux moins profondes; le hareng du Pacifique, pour sa part, a été consommé prioncipalement de décembre à mars, période qui coïncide avec la migration avant-frayage du hareng dans le détroit de Géorgie. La consommation annuelle de merlu en 1988 a été évaluée à 4 214 tonnes soit 3,5 p. 100 de la biomasse totale des stocks, ou à 71 p. 100 des prises commerciales moyennes récentes. La consommation annuelle du hareng a été évaluée à 3 206 tonnes, soit 3,2 p. 100 de la biomasse totale des stocks ou 27 p. 100 des prises commerciales moyennes récentes. Les salmonidés représentent 4,0 p. 100 du régime alimentaire des veaux marins; il s'agit surtout de saumons adultes qui se préparent à remonter les cours d'eau pour y frayer, capturés principalement dans les estuaires. Cependant, les activités de prédation axées sur la truite semblent également avoir été importantes à certains endroits. On évalue la consommation annuelle de salmonidés à 394 tonnes, soit environ 2,8 p.100 de l'évasion annuelle moyenne récents. La morue-lingue constitue 3,0 p.100 du menu; elle est capturée par les veaux marins de novembre à avril surtout, au moment où les mâles défendent leur progéniture. On évalue la consommation annuelle de morue-lingue à 294 tonnes, ce qui équivaut approximativement au total des prises commerciales et sportives récentes. Les autres proies importantes du

détroit de Géorgie sont les pilotins tachetés (3,4 p. 100 du régime alimentaire global), les ditrèmes (2,3 p. 100), les céphalopodes (2,1 p. 100), les poissons plats (1,2 p. 100), les chabots (1,2 p. 100) et les sébastes (1,1 p. 100). Les données relatives au détroit de Géorgie et l'information limitée recueillie ailleurs mettent en lumière le caractère opportuniste du veau marin, dont l'alimentation varie suivant les régions, les saisons et les proies locales disponibles.

1. INTRODUCTION

Because pinnipeds sometimes consume prey that are the target of commercial and recreational fisheries, they are viewed as competitors with man. Historically, the abundance of many pinnipeds, and hence the degree of competition, was maintained at low levels by commercial harvests and predator control programs. In recent years, however, many populations have been protected and allowed to increase toward natural levels (e.g. Bartholomew and Hubbs 1952; Chapman 1981; DeMaster *et al.* 1982; Zwanenberg *et al.* 1985; Boveng 1988; Olesiuk *et al.* in press). The recovery of these populations, in some cases coupled with the more intense utilization of fishery resources, has prompted much interest in potential conflicts between marine mammals and fisheries (Mate 1980; Contos 1982; Melteff and Rosenberg 1984; Beverton 1982; Beddington *et al.* 1985; Harwood and Croxall 1988).

In British Columbia, recent concern over marine mammal-fishery conflicts has focused mainly on the harbour seal (*Phoca vitulina*)(Malouf 1986). Earlier in this century (1913-64), harbour seal populations throughout British Columbia were maintained below natural levels by bounty kills and predator control hunts (Fisher 1952; Bigg 1969; Olesiuk and Bigg, in prep.). During 1963-68, populations were further reduced by an intense commercial harvest for pelts (Olesiuk and Bigg, in prep.). However, since the species was protected in 1970, harbour seals throughout the province have been increasing exponentially at a rate of 12.5% per annum (Olesiuk *et al.* in press). Total abundance in British Columbia was estimated to have increased from 9,000-10,500 in 1970 to 75-88,000 in 1988.

Accurate assessments of pinniped-prey interactions have generally been precluded by the lack of information on the feeding habits of pinnipeds (e.g. Lowry 1984; Melteff and Rosenberg 1984; Bowen 1985; Harwood and Greenwood 1985; Malouf 1986; Harwood and Croxall 1988). Traditionally, diets were usually assessed by examining the stomach contents of animals killed during commercial harvests or control programs, or for research (e.g. Scheffer and Slipp 1944; Mansfield and Beck 1977; Spalding 1964; Perez and Bigg 1986). Because the stomach collections were often small or concentrated in particular areas or months, they were often not representative of the entire population. For example, prior to the present investigation, knowledge of the diet of harbour seals in British Columbia was based on 69 stomachs containing food (Fisher 1952; Spalding 1964). Moreover, this small sample was probably biased as a disproportionate number of samples had been collected in the Skeena and Fraser Rivers and the vicinity of other rivers when salmon were spawning (Spalding 1964; Malouf 1986), and only 5 stomachs were collected during the period January-May. Despite the inadequacy of much of the existing data, additional stomachs have become increasingly difficult to obtain as many species of pinnipeds have been protected. This has necessitated the need for more benign methods for assessing diets.

Although direct observations of feeding pinnipeds has proved useful in very specific circumstances (Jameson and Kenyon 1977; Brown and Mate 1983; Gearin *et al.* 1988), several potential sources of bias limit the general utility of this approach: 1) feeding often occurs at night when observations are

difficult, and the prey consumed at night may differ from those taken during the day (Spalding 1964; Perez and Bigg 1980); 2) only larger prey may be brought to the surface to be consumed (Spalding 1964); and 3) the visual identifications of prey from a distance are often subjective. Another alternative is lavaging the stomachs of physically restrained or chemically immobilized animals (Antonelis *et al.* 1987). However, this method is only applicable to those pinnipeds that can be easily captured, and to the areas and months in which they can be captured. Also, the prey remains recovered by lavaging may be biased toward smaller items (Antonelis *et al.* 1987).

An increasingly popular alternative is scat (faecal) analysis (Pitcher 1980; Everitt *et al.* 1981; Bailey and Ainley 1982; Beach *et al.* 1982; Brown and Mate 1983; Hawes 1983; North *et al.* 1983; Antonelis *et al.* 1984; McConnell *et al.* 1984; Harkonen 1987; Harvey 1987; Prime and Hammond 1987; Gearin *et al.* 1988; Payne and Selzer 1989). The main advantage of this approach is that, for many species of pinnipeds, large numbers of scats can be collected in a benign and cost-effective manner. There are, however, three main problems associated with scat analyses. First, separating the undigested remnants used to identify prey from the faecal matter can be an unpleasant and time-consuming process. Second, the prey remains recovered from scat samples may not accurately reflect the true diet. For example, scat analyses based on otoliths would tend to underestimate the prevalence of: 1) fish with small or fragile otoliths which may be completely digested (Hawes 1983; Jobling and Breiby 1986; Jobling 1987; da Silva and Neilson 1985; Dellinger and Trillmich 1988; Harvey 1989); 2) larger fish, the heads along with the otoliths of which may not be consumed (Rae 1968; Pitcher 1980); and 3) cartilaginous fish which lack well-defined otoliths (Pitcher 1980; Gearin *et al.* 1988). Third, a portion of the structures used to identify prey may be completely digested, eroded beyond recognition, or reduced in size during their passage through the alimentary tract (Prime 1979; Hawes 1983; McConnell *et al.* 1984; da Silva and Neilson 1985; Harvey 1989). As a result, estimates of the amount of prey consumed based on the number and size of the structures recovered would be underestimated unless appropriate correction factors were applied (McConnell *et al.* 1984; Harvey 1989).

During 1982-88, we conducted a comprehensive study of the feeding habits of harbour seals in the Strait of Georgia and in several other regions of British Columbia based on scat analysis. The primary objectives were to assess the importance of various prey, particularly salmonids, and seasonal and regional variability in the seals' diet. A secondary objective, which we considered a prerequisite, was to develop improved methods for processing and interpreting scat samples, and analyzing scat data. In this report, we describe these methodological developments, which we have found to also be applicable to other pinnipeds (Olesiuk, unpubl. data). We also provide a detailed description of the diet and estimate annual prey consumption on a regional and seasonal basis, which we believe will be useful in formulating local management policy. Readers are referred to Olesiuk (in prep.) for a more general overview of the study.

2. SAMPLE COLLECTION AND ANALYSIS

2.1 Scat collections

Scat samples were found by searching logbooms, reefs, islets, sandbars and other substrates seals used as haulouts. Each sample was placed into a 600 ml polystyrene jar and the jars then filled two-thirds with water and covered with uniquely numbered lids. The numbered lids provided a means of recording field notes associated with the sample, such as date and location, until it could be processed, usually within a few days. In many cases, scats were found in crevices or amongst barnacles and only a fraction could be collected. In other cases, a portion of the scat may have been washed away by rain or by tides prior to collection. Thus, samples often represented only portions of whole scats.

The analyses in this report were based on a total of 3,000 scats collected between December, 1982, and March, 1989. The primary study area, wherein 2,841 (94.7%) of the samples were collected, was the Strait of Georgia (Figures 1 & 2). Samples were collected from 58 sites distributed throughout this area (Figure 2) and in all months (Figure 3). Most major haulout sites were sampled. During two aerial censuses of the study area in May-June and in August, 1988 (Olesiuk *et al.* in prep.), the sampled sites accounted for 45-46% of the total number of seals observed. Thus, the samples collected from the main study area provided a representative sample from which seasonal and regional variations in diet could be assessed.

Within the Strait of Georgia, we recognized two distinct types of habitat: estuaries and non-estuaries. Estuaries consisted of the large, shallow, soft-bottomed areas that occurred at the mouths of some rivers. In occupied estuaries, seals routinely hauled out on logbooms or on tidal sandbars. Twelve estuaries in the study area were utilized in this way by appreciable numbers ($\geq$10) of seals: Comox Harbour, Mud Bay, Fanny Bay, Deep Bay, the Nanaimo River estuary, Shoal Islets, Cowichan Bay, Mill Bay, Squamish River estuary, Port Moody, Boundary Bay and the mouth of the Fraser River (Figure 2) (Olesiuk *et al.* in prep.). Seals were widely distributed outside of estuaries and utilized approximately 250 haulout sites, which usually consisted of tidal boulders, reefs, islets, bluffs, and ledges (Olesiuk *et al.* in prep.).

Since one of our primary objectives was to assess the magnitude and distribution of salmon predation and preliminary findings indicated that salmon predation was greater in estuaries, estuaries were sampled more intensively than non-estuary sites. Scats were collected from 11 of the 12 (91.7%) estuaries and from 47 of 250 (18.8%) non-estuary sites. Of the 216 scat collections (a collection was defined as all samples collected at one site on the same date) made in the main study area, approximately half (52.3%) were obtained from estuaries (Figure 3a) and estuary collections ($\bar{x}$=17.5 samples) tended to be larger than non-estuary collections ($\bar{x}$=8.4 samples). As a result, 69% of all samples were obtained from estuaries and 31% from outside estuaries (Figure 3b).

Fewer scat samples were collected from regions outside the main study area (see Figure 1). A total of 58 samples (23 collections) were obtained from 4 sites off southwest Vancouver Island during June-October, 1988; one sample was collected in Barkley Sound in June, 1987; 10 samples (1 collection) from Gull Islet off northwest Vancouver Island in February, 1989; 49 samples (3 collections) from 2 sites at the entrance to Johnstone Strait in July and September, 1988; and 41 samples (9 collections) from 4 sites distributed throughout Masset Inlet in April and June, 1983. Although these collections were too limited to assess the overall diet or seasonal variations in diet outside the Strait of Georgia, they provided information on large-scale regional variations in diet when compared to the Strait of Georgia samples.

2.2 Processing of samples

Prior to being processed, scats were allowed to soak in the water that had been added for typically 1-4 days. During this period, the scat usually dissolved and formed a slurry on the bottom of the sample jar. As an indication of the size of each sample, the volume of the slurry was measured by holding the sample jar next to a calibrated jar. A functional regression between the volumes (*VOL* in ml) and fresh wet-weights (*WWT* in gm) for a subsample of 152 scats indicated that the former provided a reliable index of the latter:

$$[1] \quad WWT = 5.171 + 0.7634 \cdot VOL \qquad (r^2=0.793;\ P<0.01)$$

Sample volumes ranged from trace (<5ml) to 825 ml ($\bar{x}$=85.9 ml), which corresponded to wet weights of <9 to 635 gms ($\bar{x}$=70.7 gms). Volumes were not recorded for 128 (4.3%) of the samples.

Undigested prey remnants were separated from other faecal matter with the aid of an elutriator. The elutriator operated on the principle that, owing to the differences in their density and solubility, the skeletal and other hard parts of prey could be separated from the remaining faecal matter in a flowing column of water. Bigg and Olesiuk (in prep.) describe the elutriation system and its operation in detail. Elutriation typically reduced the total volume of samples by 70-90% ($\bar{x}$=83.4%), whereas recovery trials indicated that 90-100% ($\bar{x}$=98.3%) of various fish skeletal elements and 70-100% ($\bar{x}$=85.0%) of cephalopod beaks were retained (Bigg and Olesiuk in prep.). The loss of most scales during elutriation was not considered a major drawback because scales, when present, were generally abundant and only useful for establishing the presence of prey.

Following elutriation, samples were briefly rinsed with hot water on a 320 μm sieve, dried in paper towels under heat lamps, and stored dry in 15 X 900mm plastic petri dishes. At this stage, samples had usually been reduced to the indigestible prey remains and a small amount of relatively odourless, ash-like material. Samples could be stored in this condition for several years without deterioration.

2.3 Sample interpretation

The prey represented in each scat were identified by comparing undigested skeletal fragments and other hard parts (e.g. cephalopod beaks, teeth, scales) to reference material. Identifications were made primarily by two of us (SJC and BJW) using a reference collection compiled by the Department of Anthropology, University of Victoria. The collection contained approximately 350 specimens representing 120 species of fishes from 40 families. An additional 10 species not represented in the University collection were loaned from the Royal British Columbia Museum (formerly the British Columbia Provincial Museum) in Victoria.

Insofar as possible, all of the elements present in samples were identified as to what structure they were and keyed to the lowest possible taxonomic level. A wide array of structures including otoliths, teeth and cranial bones, as well as members of the branchial arch and axial, appendicular, and caudal skeletons, proved useful for identifying prey (see Appendix I). As discussed later (see Sections 4.3 and 5.1), the utilization of this diverse range of structures was considered a significant improvement over previous scat studies, which relied primarily on otoliths. All elements in the sample were usually enumerated, and those belonging to each prey taxa transferred to separate petri dishes. When there was a very large number of elements, a subsample was counted and the total number subjectively estimated. For some structures that were difficult to count, such as scales, only their presence or minimum number present was recorded. The size of structures was also noted and categorized (i.e. tiny, small, medium, and large) relative to the potential size range for each prey species. These size categories, albeit crude and subjective, were nevertheless useful. For example, tiny salmonid elements represented smolt-sized fish, small elements represented juvenile-sized fish, and medium and large elements represented adult-sized fish. Placing the elements of each prey taxa into separate petri dishes proved useful when it was later necessary to confirm identifications or obtain additional information. With experience, each sample required an average of approximately 20 minutes to be examined.

Identifications were considered to have been conservative in that prey were more likely to have been classified as unidentifiable rather than to an erroneous family, or were keyed only to the family level rather than as a tenuous species. A blind test was conducted to evaluate the accuracy of identifications. Forty-seven skeletal elements typical of those recovered in scats, representing 15 different structures from 21 species of marine fishes, were selected by one of us (PFO) from a reference collection at the Pacific Biological Station, and subsequently independently identified by BJW and SJC (see Section 5.1b).

All scat samples were also scanned for magnetic coded-wire fish tags, but none were detected.

3. DATA ANALYSIS

3.1 Relative importance of prey

Two basic types of indices have been used to measure the importance of prey in pinniped diets: frequency of occurrence and relative volumes. In frequency of occurrence, the importance of a given prey species is estimated by dividing its total number of occurrences (i.e. number of samples in which it occurs) by the total number of occurrences of all prey species in all samples. The underlying assumption is that all prey species occurring in samples were consumed in equal quantities. The index therefore tends to exaggerate the importance of incidental prey that were consumed in small quantities and underestimate the importance of focal prey consumed in large quantities. The index may also be biased if traces of prey are retained in stomachs over several feeding bouts, as has been shown for cephalopod beaks (Bigg and Fawcett 1985).

In volumetric analyses, the importance of a given prey species is estimated by dividing its total volume in all samples by the total volume of all prey in all samples. The underlying assumption is that the relative volumes of prey in stomachs reflect the volumes actually consumed. The index therefore tends to underestimate the importance of soft-bodied prey, which are digested rapidly, and overestimate that of firm-bodied prey which are digested more slowly. The volumetric index is also more prone than the frequency index to biases resulting from diurnal feeding patterns because prey are reduced in volume more rapidly than they are completely digested. For example, samples collected during daylight would tend to underestimate the importance of prey species consumed at night and overestimate the importance of prey species consumed during the day. Finally, the volumetric index is also more susceptible to small-sample biases in that it may be distorted by a few samples containing large volumes of undigested prey.

For the current study, we developed a new index, referred to as split-sample frequency of occurrence, which we considered to be appropriate for assessing the relative importance of prey from scat data. The index was predicated on two key assumptions: 1) the prey identified in scat samples represented all those consumed in the previous meal; and 2) all prey species comprising a meal had been consumed in equal volumes. Thus, the proportion of the total diet comprised of the kth prey species, P_k, in a collection of scats, i=1,..N, was estimated by:

$$[2] \quad P_k = \sum_{i=1}^{N}(O_{ki}/\sum_{k=1}^{n}O_{ki})/N \qquad k=1,..,n \text{ } (n=\#\text{ different prey species})$$

where O_{ki} is a binary variate that indicated whether the kth prey species was absent or present (0=absent and 1=present) in the ith sample, such that ΣO_{ki} represented the total number of prey species present in the ith sample. Thus,

if only one prey species occurred in a sample it was scored as 1, if two prey species occurred each was scored as 0.5, and so forth. *N* represents the sum of scores of all prey species in all samples or, equivalently, the total number of samples.

Conceptually, the split-sample frequency index is intermediate to frequency of occurrence and volumetric indices. It resembles the former in that, firstly, it only required data on the presence or absence of prey and, secondly, all samples are weighted equally in the index. The first property was critical because we concluded that the absolute volumes of prey consumed could not be gleaned from scat contents (see Section 5.1e); and the second property was important because the scat samples often represented only subsamples of whole scats which varied considerably in size. On the other hand, the split-sample index resembles volumetric analysis in that prey comprising an entire meal (which were presumably consumed in greater volumes) score higher than prey that formed only a portion of a diverse meal (which were presumably each eaten in smaller volumes).

As a test of the general validity of the split-sample index, we applied the procedure to stomach content data collected on the northern fur seal (*Callorhinus ursinus*), and compared the results to conventional frequency and volumetric analysis. The northern fur seal data base was considered suitable for this purpose as it represented the largest stomach content data base for any pinniped (10,699 stomachs containing food) and both the presence and the volume of prey species had been recorded. The data were collected during 1958-74 jointly by Canada and the United States as part of research contributions to the North Pacific Fur Seal Commission. Perez and Bigg (1980, 1986) described the fur seal data in detail and presented conventional frequency and volumetric diet analyses. We limited the comparison between our split-sample frequency index and the conventional indices to the importance of fish prey, because the incidence of cephalopods in stomachs was known to have been biased by the retention of beaks and, due to differences in their digestibility, fish and cephalopod volumes were not directly comparable to one another (Bigg and Fawcett 1985; Bigg and Perez 1985). The comparison was conducted on both a regional basis (see Perez and Bigg 1986) and for all regions combined.

As expected, the split-sample index gave estimates that were intermediate to conventional frequency and volumetric indices (Figure 4). Even though the split-sample index was calculated exclusively on the basis of the presence or absence of prey, it conformed closely with volumetric analyses on both a regional basis (r^2=0.929; Figure 4a) and when all of the regions were combined (r^2=0.978; Figure 4b). On average, the split-sample index, relative to the volumetric index, tended to underestimate the importance of prey that comprised large portions of the diet and overestimate the importance of those that comprised small portions of the diet, but the differences were small. For example, the functional relationship between the estimates of the two indices indicated that a prey species that comprised 50.0% of the diet by volume within a region comprised 48.5% by split-sample frequency. Moreover, the improvement in the degree of correlation between the two indices when all regions were combined indicated the discrepancies were not systematic with species (i.e. the differences for a particular prey species within regions tended to cancel when all regions were pooled).

The potential biases that may arise in applying the split-sample frequency index to scat content data are addressed further in Section 5.1.

3.2 Seasonal and regional variations in diet

As outlined in Sections 5.2 and 5.3, diets typically varied with location and, at a given location, with season. To account for this variability, data were stratified both temporally and spatially.

Seasonal variations in diet were accounted for by evaluating diet composition on a monthly basis. The diet in a given month was estimated by pooling all samples collected in that month as well as all samples collected in the last half of the preceding month and first half of the proceeding month. Samples from the preceding and proceeding months were included for three reasons. First, sampling intervals in some cases were slightly greater than one month, such that sites not sampled in a particular month were often sampled late in the preceding month and/or early in the proceeding month. Second, scats may have accumulated at some sites, so those collected early in a month may have actually been deposited in the preceding month. Third, because the monthly estimates represented offset two-month running means, irregularities arising from small sample sizes tended to be smoothed.

Regional variability in the diet was accounted for by stratifying samples by area. Two different areal stratification schemes, referred to as the low-level and high-level schemes, were applied. For the low-level scheme, all samples collected in estuaries were pooled together as were all samples collected outside estuaries. This resulted in a total of 24 strata (2 areal X 12 months). Owing to the disproportionate sampling effort for estuaries and non-estuaries (Figure 3b), this was considered the lowest valid level of stratification. The main advantage of this scheme was that it provided relatively precise estimates since relatively large numbers of samples had been collected from each of the 24 strata (Figure 3b). While precise, the low-level estimates were subject to inaccuracies as no provision was made for differences in diet among estuaries or among non-estuary sites.

For the high-level scheme, each estuary was considered as a separate strata. Exceptions were Boundary Bay and the Fraser River which were pooled; and Deep, Mud and Fanny Bays which were also pooled. These estuaries were pooled because of their close proximity to one another (Figure 2) and it was possible seals may have moved between them over short time intervals, feeding in one and later hauling out and defecating in another. Because seals were widely dispersed outside estuaries, the non-estuary sites were stratified into three latitudinal geographic areas (Figure 2), the boundaries of which corresponded with the subareas surveyed during aerial censuses (see Olesiuk *et al.* in press, in prep.). The high-level scheme thus consisted of a total of 144 strata (12 areal [9 estuaries and 3 non-estuary regions] X 12 months). However, several estuaries were vacated during some months, so only 103 of the 108 (95.4%) strata were occupied by appreciable numbers ($\bar{x} \geq 10$) of seals.

The two advantages of the high-level stratification scheme were that it provided more accurate estimates since the variations in diet among estuaries and non-estuary regions were taken into account, and it allowed prey consumption to be calculated on an estuary-by-estuary and regional basis. The disadvantage of the high-level estimates was reduced precision owing to the smaller sample sizes available for each strata. In fact, no samples were collected from 22 of the 103 (21.3%) occupied estuary strata and 3 of the 36 (8.3%) non-estuary strata. In these cases, we applied the overall diet for all other strata in the same class (i.e. estuary or non-estuary) for that month. For instance, if an estuary was not sampled in January, we applied the estimate for all the estuaries sampled in January. These extrapolations had little effect on the overall diet as the sampled strata accounted for 78.6% of the seasonally-weighted total abundance of seals in estuaries and 91.7% of the total abundance outside estuaries.

Due to the lack of sufficient sample sizes, we made no attempt to account for inter-annual variations in diet (i.e. data from all years were pooled). However, an informal comparison between the strata that were sampled in different years indicated seasonal and regional variations in the diet were much more pronounced than any among-year differences.

3.3 Absolute importance of prey species

The absolute importance of a prey species is a function of both its relative importance in the diet and the number of seals feeding on it. For example, a particular prey may be relatively important in the diet within a strata (i.e. area and month), yet would be of little absolute importance if the strata were occupied by few seals. Conversely, a particular prey might only constitute a small proportion of the diet, but be of high absolute importance if it were to contribute to the diet of enough seals.

The absolute importance of the kth species in the jth strata, expressed in terms of annual biomass consumed, C_{kj}, was estimated by integrating estimates of diet composition, seal abundance and feeding rates:

$$[3] \quad C_{kj} = \int_{t=1}^{t=365} N_{jt} \cdot P_{kjt} \cdot F \, dt$$

where N_{jt} is the estimated number of seals within the jth strata on the tth date (1=January 1st; 365=December 31st), P_{kjt} the proportion of total diet comprised of the kth prey species in the jth strata on the tth date, and F an estimate of the mean per capita daily food requirements. N_{jt} was linearly interpolated between consecutive censuses of each strata and P_{kjt} was linearly interpolated between monthly mean estimates of diet (as per Sections 3.1 and 3.2), which we assumed were indicative of the midpoint of each month. The integral was solved

by calculating its finite approximation using daily Δt increments.

Mean daily per capita food requirements, F, were estimated from two sources of information: 1) values of energetic parameters for captive phocids reported in the literature; and 2) the volumes of undigested prey found in the stomachs of harbour seals collected on the east coast of Canada (Boulva and McLaren 1979). In both cases, food requirements were estimated for each sex- and age-class in the population, and the estimates subsequently weighted according to the sex- and age-structure of the population (Bigg 1969; Olesiuk in prep.). The energetic calculations are described and the corresponding energetic life tables given in Olesiuk (in prep.).

Aerial censuses were conducted to determine the abundance and distribution of seals (Olesiuk *et al.* in press, in prep.). Based on two complete censuses of the Strait of Georgia study area in May-June and in August, 1988 (with adjustments for unborn pups), the total population at the end of the 1988 pupping season, N_p, was estimated to be 15,810 (Olesiuk *et al.* in press). Because the population increases during the pupping season due to recruitment and decreased throughout the year due to mortality, N_p represents the seasonal maximum size of the population, which was attained on t=p=250 (6 September).

Because suitable tides for aerial censuses were not available during winter months, it was not possible to monitor the seasonal fluctuations in population size. Alternatively, the seasonal fluctuations were modeled based on estimated recruitment and mortality rates. We assumed the Strait of Georgia population was closed to immigration and emigration, which was realistic considering that harbour seals are generally non-migratory (Bigg 1981) and the study area was relatively large. Moreover, any movements of seals between the study area and neighbouring areas in British Columbia were likely minimal as the density of seals in the latter were much lower compared to the Strait of Georgia (Olesiuk *et al.* in press). The mean annual per capita mortality rate, m, was calculated from the finite annual population growth rate (λ=1.125; Olesiuk *et al.* in press) and the birth multiplication rate (β=1.25; Bigg 1969; Olesiuk *et al.* in press):

$$[4] \quad m = (\beta-\lambda)\cdot\beta^{-1} = 0.10$$

Assuming that mortality was uniformly distributed throughout the year, the finite annual mortality rate was transformed to an instantaneous daily mortality rate, Z:

$$[5] \quad Z = \{-\ln(1-m)\}\cdot 365^{-1} = 0.0002887$$

Fluctuations in population size due to recruitment were modeled by dividing the maximum post-pupping population, N_p (15,810) by B_t, defined as the birth multiplication rate, β, less the proportion of the pups that had been born by a given date. As pupping was normally distributed with a mean birth date, μ,

of 208 (27 July) and σ of 16.1 days (Olesiuk *et al.* in press), B_t was given by:

$$[6] \quad B_t = 1.25 - \int_{-\infty}^{\frac{t-\mu}{\sigma}} 2\pi^{-0.5} e^{\frac{(t-\mu)^2}{2\sigma^2}} dt \cdot 0.25$$

The size of the population on a given date, N_t, was therefore estimated as:

$$[7] \quad N_t = (N_p/B_t)e^{-Z(t-p)}$$

and, accordingly, the mean annual size of the population, $\bar{N}$, as:

$$[8] \quad \bar{N} = 365^{-1} \cdot \int_{t=1}^{t=365} (N_p/B_t)e^{-Z(t-p)} \, dt$$

which we solved by calculating a finite approximation using daily Δt increments.

Although it was not possible to monitor the population in the entire study area throughout the year, seals within estuaries could be censused during all months. Aerial censuses were feasible in estuaries because seals hauled out on logbooms at various tidal levels, and we could count swimming seals in these confined, shallow areas. Between May, 1988, and February, 1989, we conducted a series of 5 aerial censuses, at roughly equal intervals, of all estuaries except for Port Moody, which could not be flown due to its proximity to a major airport, and the Squamish River, which was excluded owing to its distance from other estuaries. The aerial counts were also supplemented with periodic boat and land counts; and Port Moody and the Squamish River with additional counts provided by local residents (R. McVicar, Port Moody, & C. Tamburri, Squamish, pers. comm.). The census methods and data are described in greater detail in Olesiuk *et al.* (in prep.). Seasonal changes in overall seal abundance outside estuaries was calculated indirectly by subtracting the total count for estuaries from the estimated total size of the study area population [equation 7], but we had no way of determining seasonal movements among the non-estuary regions.

4. PREY SPECIES

4.1 Scat contents

Eighty-three (2.8%) of the 3,000 scat samples were devoid of identifiable prey. A disproportionate number (16.9%) of the empty samples were collected from Mill Bay in May and July. Although the Mill Bay samples, many of which were voluminous, contained nothing we considered to be potential prey, most contained traces of vascular plants (*Carex lyngbyei*) and/or algae (*Ulva* spp. and possibly *Zostera marina*). We suspect that seals in this estuary may have been feeding on roe deposited on the plants or on soft-bodied prey among the plants, and that the plants were inadvertently ingested. The remaining empty samples were widely distributed in collections from various sites and months, and the absence of identifiable prey was in most cases probably attributable to their small volumes ($\bar{x}$=21 ml)(see Section 5.1c).

A total of 5,109 prey items were identified in the 2,917 samples containing identifiable prey. Although samples occasionally contained as many as 7 prey species, most (80.8%) contained only one or two ($\bar{x}$=1.82) (Figure 5). The actual diversity of meals was probably slightly greater than depicted in Figure 5, as only a portion of the prey consumed may have been represented in small-volume samples. Based on the corrections for this bias derived in Section 5.1, we estimated that 6.3% of all prey items were absent as a result of the small-volumes. This being the case, meals would actually have been comprised of a mean of 1.94 prey species.

Marine and anadromous fishes accounted for 5,109 (96.0%) of all the prey items identified and were by far the most prevalent prey category. The diet included at least 48 species from 20 families (Table 1). Again, the true diversity was probably greater than indicated as only 4,026 (78.8%) of the fishes were keyed to species-level. The remaining 1,005 (19.7%) fishes keyed only to family and the 78 (1.5%) only to class may have been comprised of several species or of several families respectively (Section 4.2). The two most predominant families were the gadoids and clupeids, which occurred in 61.1 and 58.1% of all samples that contained identifiable prey respectively. Other important families, in decreasing order, were the salmonids, batrachoids, embiotocids, cottids, pleuronectids, hexagrammids, scorpaenids, ammodytids and osmerids, each of which occurred in 1.6-15.5% of all samples containing identifiable prey. The remaining 9 families each occurred in <1% of the samples.

The second most prevalent prey category was cephalopods, which occurred in 178 (6.1%) of the samples that contained identifiable prey and represented 3.5% of all prey items identified. Although most samples (61.9%) containing cephalopods also contained their beaks that could potentially be keyed to species or genus, we lacked the necessary expertise. However, a superficial examination of the beaks indicated that the vast majority were squid (mainly *Loligo opalacens* with some *Gonatus* spp.), but at least one octopus was also present.

The remaining prey categories were considered unimportant as they occurred in <1% of the samples containing identifiable prey and accounted for <0.5% of the total number of prey items identified. Twenty-four samples con-

tained crustaceans: 19 were crabs, 4 were shrimp and one was unidentified. No attempt was made to key these to lower taxonomic levels. Other invertebrates were found in 10 samples. One sample contained a large quantity of pulverized mussel shell and 3 contained sea urchin spines. Six samples contained numerous small chitinous structures that were probably the mouth or appendage parts of an unidentified invertebrate (crustacean mandibles?), or possibly the beaks of a cephalopod with which we were not familiar. We subsequently refer to this unknown invertebrate as Species 'N'. Bird remains were found in 3 scat samples.

Scat samples also occasionally contained traces of algae, barnacle fragments, and small amphipods, bivalves and gastropods. We subjectively considered that these items were either inadvertently collected with the sample or represented secondary prey from the gut of primary prey, and thus excluded them from further analysis. In any event, these items were too small and present in insufficient quantities to have contributed significantly to the diet.

The diversity of prey identified in scat samples compared favourably with the prey identified in the stomachs of harbour seals collected in the Pacific Northwest. All but one of the 19 prey types reported in the 69 stomachs collected in British Columbia (Fisher 1952; Spalding 1964) were represented in our scat samples. The exception was sablefish (*Anoplopoma fimbria*), which occurred in 2 stomachs. Similarly, all but 2 of the 22 prey types reported in the 81 stomachs collected in Washington State (Scheffer and Sperry 1931; Scheffer and Slipp 1944) were represented in our scat samples. The two exceptions were burrowing crayfishes (*Upogebia pugettensis* and *Callianassa californiense*) and ratfish (*Hydrolagus colliei*), which occurred in 3 and one stomachs respectively.

4.2 Precision of identifications

The precision of prey identifications varied among taxa, which dictated how data were subsequently interpreted.

Gadidae: Of the 1,785 gadoids identified, 1,599 (89.6%) could be keyed to species-level. All 4 gadoids endemic to waters off British Columbia (Hart 1973) were represented. Of the remaining 186, 97 (52.2%) were identified as one of the 3 species other than hake. Since the 4 species of gadoids were roughly equally identifiable, we partitioned the unidentified gadoids among species based on the relative prevalence of those that were identified to species-level. First, the unidentified non-hake gadoids were partitioned among the other 3 species and, second, the remaining unidentified gadoids were partitioned among all 4 species.

Clupeidae: All of the 1,694 clupeids identified in samples could be keyed to species-level.

Salmonidae: Very few (1.6%) of the salmonids could be keyed to species-level because their otoliths were rarely recovered and other structures were not diagnostic of species unless in pristine condition. In most, but not all, cases, Pacific salmon (*Oncorhynchus*[1] spp.) could be discerned from trouts (*Salmo* and *Salvelinus* spp.[1]) by subtle differences in the porosity of their vertebrae or the shape of their lingual plates and premaxillae. Thirty-four (7.5%) of the salmonids were identified (sometimes tentatively - see below) as trouts, and the remainder were assumed to be Pacific salmon. Since the features used to distinguish these genera were not always well-preserved, the actual proportion of trouts was probably slightly underestimated and that of Pacific salmon slightly overestimated.

Five collections, 3 from Comox Harbour during May-July and 2 from Port Moody in September-November, warrant special comment. At each site, two distinct size-classes of salmonids were represented in the scats. In Comox Harbour, the smolt-sized salmonids were tentatively identified as *Salmo* spp. and most of the adult-sized salmonids as *Oncorhynchus*. Similarly, in Port Moody the juvenile-sized salmonids were tentatively identified as *Salmo* spp. and all of the adult-sized salmonids as *Oncorhynchus*. However, because the structures of the smaller salmonids were minuscule and our reference material deficient in salmonids of this size-range, it was possible that we may have mis-interpreted the features considered to be trout-like or the differences may actually have been ontogenetic rather than phylogenetic.

The species within each genera could not usually be distinguished, and some species were more distinctive than others. For example, chinook salmon were more likely to be recognized as such because of their large otoliths and chum salmon because of their well-developed teeth. Conversely, sockeye were less likely to be identified due to their small otoliths. In view of these biases, the identified species probably did not accurately reflect the actual species composition.

Batrachoididae: All of the 234 Batrachoids were identified as plainfin midshipman, the only species endemic to the study area (Hart 1973).

Embiotocidae: Of the 221 embiotocids identified, 192 (86.9%) were keyed as one of two species, and 2 were identified as a third but unknown species that was not represented in the reference collection. Since all species of embiotocids were about equally identifiable, we partitioned the 27 that could only be identified to family-level among the 3 species based on their relative prevalence.

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[1]For convenience, we adopted traditional nomenclature and refer to Pacific salmon as *Oncorhynchus* and Pacific trouts as *Salmo/Salvelinus*. Although taxonomically less accurate (Smith and Stearley 1989), this system was preferred as we could usually distinguish between these genera, but not between species within each genera.

Cottidae: Only 92 (57.9%) of the 159 cottids could be keyed to species-level. Since the species, or at least the genera, within this family were generally quite distinctive, the majority of the unidentified specimens were probably species not represented in the reference collection, which contained only 15 of the 42 species endemic in the study area (Hart 1973). Thus, no attempt was made to estimate the species composition of the sculpins consumed.

Pleuronectidae (and possibly Bothidae): Only 25 (16.7%) of the 150 flatfishes were identified to species-level, mainly because we felt the effort involved could not be justified. Even though all those identified were pleuronectids, this category probably also included some bothids, which have been reported in the diet of harbour seals adjacent to our study area (Everitt *et al.* 1980; Brown and Mate 1983; Harvey 1987). The disproportionate number of starry flounder identified likely exaggerated their actual prevalence in the diet, as many were keyed on the basis of their distinctive scutes which other species lacked. For the above reasons, we made no attempt to estimate the species composition of the flatfishes consumed.

Hexagrammidae: Eighty (96.3%) of the 83 hexagrammids identified were identified as either lingcod or greenlings, but the greenlings could not be identified to species or family. The 3 unidentified hexagrammids were partitioned among the two categories according to their relative prevalence.

Scorpaenidae: No scorpaenids were keyed to species-level because we felt the effort involved could not be justified and many of the structures used in the identifications were not diagnostic among species.

Ammodytidae: All ammodytids were identified as being Pacific sandlance, which is the only member of the family endemic to the study area (Hart 1973).

Osmeridae: Thirty-one of 46 (67.4%) smelts were keyed to species-level and all but two of these were eulachon. Although eulachon was undoubtedly the most predominant smelt, its predominance was probably overestimated as several species of smelt were not represented in the reference collection.

Other fishes: Little effort was made to key the remaining fishes to species-level as they occurred in so few samples. However, for some families (e.g. gasterosteidae, anarchichadidae) only one member was endemic to the study area. Although both pholids and steichaeids were identified, these two families were difficult to distinguish from one another and there were potentially errors in the assignments between them.

Unidentified fishes: There were two distinct categories of unidentifiable fishes. Eleven samples contained very distinctive elements that could

not be identified, and almost certainly belonged to species not represented in the reference collection. These elements represented 8 different species that may or may not have been members of the previously identified families. We subsequently refer to these as "other" fishes.

Sixty-seven samples contained fish remnants that were too indistinctive or eroded to key, but which did not originate from the other prey species identified in the sample. For example, very large eye lenses may have been found in samples that otherwise contained only very small fishes. The unidentified fishes were probably comprised of a diverse mixture of the species that had previously been identified in other samples, but may also have represented some "other" fishes. We subsequently refer to these as "unidentifiable" fishes.

4.3 Structures used in identifications

A wide array of structures proved useful for identifying prey. We relied upon beaks, pens and eye lenses to identify cephalopods; and spines, mouth and appendage parts, and carapace and valve fragments to identify invertebrates. A total of at least 90 structures, which is a minimum as members of some series of elements were not always differentiated from one another, were utilized to identify fish prey (see Appendix I). As a result, prey identifications were generally based on many elements ($\bar{x}$=38.7) and on several different structures ($\bar{x}$=3.44) (Table 2). As discussed in Section 5.1d, we believe that using such a wide array of structures minimized the probability of prey not being detected because certain structures had been completely digested or because only selected parts of the prey had been consumed.

Otoliths, which have been used extensively by other investigators, proved to be of limited value in the present study. Otoliths accounted for only 7.1% of the total number of fish elements identified and were present in only 41.9% of all fish identifications. Moreover, only 67.5% of the different fish species identified were represented by otoliths, and the proportion of samples containing otoliths varied among species (Figure 6). Consequently, otoliths by themselves provided an incomplete and biased representation of the actual diet.

The probability of a fish being represented by otoliths was probably dependent on two principal factors: otolith size and number consumed. As has been noted by many authors (Hawes 1983; Jobling and Breiby 1986; Jobling 1987; da Silva and Neilson 1988; Dellinger and Trillmich 1988; Harvey 1989), species with large, robust otoliths (e.g. gadoids) were more likely to be represented than those with small, fragile otoliths (e.g. herring). However, another but hitherto unrecognized factor was likely the total number of otoliths consumed in a meal, which would largely be a function of the size of prey. Although a greater proportion of gadoid otoliths than herring otoliths might be recovered, more of the latter would likdely be consumed in a single meal. This might explain why roughly equal proportions of gadoids and herring were represented by otoliths (Figure 6). It would also explain why the probability of fishes being represented by otoliths was highest for smaller species with robust

otoliths (e.g. plainfin midshipman and surfperches) and lowest for larger species with fragile otoliths (e.g. salmonids and hexagrammids)(Figure 5). These trends were also evident on an intra-specific basis depending on the size of prey. For example, salmonid otoliths occurred in 64.7% of the samples containing smolt-sized salmonids, compared to only 12.3% of the samples containing larger salmonids.

The scarcity of otoliths of larger prey may have in part been due to their heads being discarded prior to being consumed, but this was generally not the case. Although otoliths were rarely found, other cranial structures (e.g. TEE, BRA, GRK; see Appendix I) were often present. For example, cranial structures were present in 75.2% of samples containing salmonids, compared to only 16.5% for otoliths; and cranial structures in 95.2% containing hexagrammids, compared to only 16.9% for otoliths. Alternatively, these results may indicate that seals consumed much of the head except for the cranium containing the otoliths, as has been observed on occasion for seals feeding on salmon (G. Ellis, unpubl. data).

One of the most useful structures for identifying prey was vertebrae (i.e. VER, UVE, VEF, ATL and VEP; see Appendix I), which accounted for 67.8% of the total number of structures identified. Vertebrae occurred in 75.4% of all fish identifications and 82.5% of the different species identified were represented by vertebrae. Although the proportion of samples containing vertebrae varied among species, the variability was much less pronounced than for otoliths. For examples, vertebrae were present in 62.7% of the samples with salmonids, 70.1% with gadoids, 86.8% with herring, and 55.4% with hexagrammids. Thus, vertebrae gave a more complete and less biased representation of diet than otoliths. The main shortcoming of vertebrae was that often they could only be keyed to family-level. In the present study, this was particularly problematic for the salmonids because they were rarely represented by otoliths and their vertebrae were not diagnostic of species.

Very specific structures proved useful for identifying some taxa. For examples, teeth were especially useful for lampreys and cartilaginous fishes, prootics for clupeids, interhaemel spines for flatfishes, and pterygiophores for rockfishes. However, caution must be exercised in interpreting this information. While these structures may be useful for establishing the presence of prey, they may not provide an accurate representation of species composition since some species may be more distinctive than others. For example, starry flounder were more easily keyed than other flatfishes due to their distinctive scutes, and staghorn sculpins more easily than other sculpins due to their distinctive pre-opercular spine. It would therefore be invalid to partition the unidentified species among species solely on the basis of these structures.

Several lines of evidence indicated that the elements recovered from scats represented only a portion of those actually ingested. The condition of elements ranged from pristine to barely recognizable, and some had undoubtedly been completely digested, or at least digested beyond recognition. Furthermore, crude calculations analogous to those given in McConnell *et al.* (1984) indicated that there were far too few structures in the scat samples to account for their volumes. Finally, the ratios of various structures deviated from the values expected on the basis of their ratios in whole prey. For example, mean vertebrae

to otolith ratios were 15.8:1 for herring and 8.2:1 for gadoids, much lower than the expected ratios of approximately 26:1 for both species (Hart 1973).

Overall, no single structure proved to be adequate for identifying all prey. We would therefore encourage that as diverse an array as possible be employed in future studies.

5. DIET COMPOSITION

In this Section, we examine the diet composition on a regional and seasonal basis. Prior to doing so, however, we assess the validity of the assumptions underlying the analysis and, insofar as possible, derive adjustments to account for possible violations.

5.1 Validity of assumptions

The accuracy of our estimates of the relative importance of prey (equation [2]) are contingent upon the following assumptions:

a) The prey present in scat samples represented those consumed in the previous meal.

Tagging studies have shown that harbour seals spend much of their time in the water (66% Sullivan 1979; 40-65% Pitcher and McAllister 1981; 63% Yochem *et al.* 1987; and 69% Thompson *et al.* 1989), and foraging may therefore be dispersed over time. Indeed, Spalding (1964) was unable to discern any diurnal foraging pattern for harbour seals and concluded that, unlike the other pinnipeds examined, harbour seals foraged throughout the day. Since foraging bouts were likely diffuse, we defined a meal as the prey consumed within a 24-hour period.

Captive studies indicate that fish otoliths are generally passed through the gastro-intestinal tract of seals within 5-30 hrs (Pastukhov 1975; Helm and Morejohn 1979; Prime 1979; Bigg and Fawcett 1985; Prime and Hammond 1987; Harvey 1989). For examples, Harvey (1989) found that 90% of the otoliths of various species were passed within 24 hours and Dellinger and Trillmich (1988) found that few otoliths were passed later than 30 hours after feeding. Thus, it was likely that most of the fish remains recovered in the scat samples had been consumed in the previous 24-hour period. Fiscus and Baines (1966) suggested that bones of larger fishes were retained in stomachs of sea lions over several feeding bouts, but gave no supporting evidence. In contrast, one of us (PFO, unpubl. data) examined the stomach contents of California and Steller sea lions

that had been feeding on hake, which have very large otoliths, and found that the number of otoliths corresponded closely with the number of eye lenses and smaller bones, which had unlikely accumulated. Similarly, Dellinger and Trillmich (1988) found that size had no effect on the passage rate of otoliths in sea lions and fur seals. Moreover, Harvey (1987) concluded that any bones retained in stomachs for >13 hours were likely to be completely digested. Nevertheless, it is possible that a few of the fish remnants recovered from the scats may have been consumed a day or two prior to the last meal. However, since the diet typically varied gradually with season (Sections 5.2 & 5.3) similar prey were likely consumed on consecutive days, so we did not consider this a serious source of bias.

The structures of prey other than fish, most notably the beaks of cephalopods, may accumulate in stomachs for periods of at least several days (Bigg and Fawcett 1985) and their presence in scat samples may not necessarily indicate they were consumed in the previous meal. However, this was not considered an important bias in the present study, as cephalopods occurred in relatively few samples (3.6%), and in most instances (68.4%) the beaks were accompanied by cephalopod eye lenses, which were likely passed rapidly. Nevertheless, this potential source of bias would warrant further scrutiny in situations where cephalopods constituted an important part of the diet.

b) The prey remnants in scat samples were accurately identified.

A blind test was conducted to assess the accuracy of identifications (Section 2.3), with the following results:

	BJW:	SJC:
Correctly identified (species-level)	30	33
Correctly identified (family-level)	16	13
Could not be identified	1	0
Error in identification	0	1

The single error, which represented an error rate of 1.1%, consisted of a hexagrammid quadrate that was mistakenly identified as a scorpaenid quadrate. All hexagrammid and scorpaenid identifications, none of which were based solely on quadrates, were subsequently reviewed. Since prey were usually identified on the basis of several different structures (Table 6), the actual error rate was probably less than indicated by the blind test.

c) The prey identified in scat samples represented all those that had been consumed in the previous meal.

Some prey species consumed in the previous meal may not have been represented in the scat sample for two reasons: 1) our samples represented only a subsample, and in some cases only a very small subsample, of whole scats; and

2) the remains of some prey species, particularly smaller or fragile species, may have been completely digested or digested beyond recognition. We address the first source of bias in this Section, and the second source in the following section.

A regression between the number of prey species identified in each sample, N_{SP_i}, and the volume of samples, *VOL*, indicated that N_{sp} tended to increase with *VOL* (t=6.789; P<0.01). However, the low correlation coefficient (r^2=0.016) indicated the relationship was non-linear, but could be more aptly be described by an asymptotic regression (Snedecor and Cochran 1980):

$$[9] \quad \hat{N}_{sp} = A - B(e^{-C \cdot VOL})$$

with asymptote A=1.905 (SE=0.038), B=0.629 (SE=0.087) and C=0.067 (SE=0.027) (Figure 7).

The asymptotic regression implied that the smaller samples provided an incomplete account of the prey consumed. For example, the very smallest samples (*VOL*<5ml) typically contained only 67% as many prey as the largest samples. However, the mean number of prey increased rapidly with volume, such that 50ml samples contained 99% of the asymptotic number. Based on the asymptotic regression [9], we derived a weighting factor, W_i, for each ith sample:

$$[10] \quad W_i = \hat{N}_{SP_i} / A$$

and accordingly weighted each sample in equation [2]. The mean weighting factor for the 2,872 samples for which volumes were recorded was 0.937, which implied that 6.3% of the prey species consumed were not represented in scats as a result of the small sample-volumes. We applied the mean weighting factor to the 128 samples for which volumes were not recorded.

The diversity of prey identified in scats compared favourably with the diversity found in stomachs. Spalding (1964) reported 110 prey items (including unidentified items) in the 69 harbour seal stomachs with food collected in British Columbia whereas Scheffer and Slipp (1944) reported 199 prey items (excluding incidental items) in the 81 stomachs with food collected in Washington State. The overall mean number of prey items in the stomachs (2.06) was similar to the asymptotic number identified in our scat samples (1.91).

d) All prey species consumed were equally represented in scat samples.

A potentially serious bias may arise in scat analyses if the recovery rates of the structures used to identify prey vary among species (Jobling and Breiby 1986; Jobling 1987). Many captive studies have indicated that otolith

recovery rates tend to be lower for species with small, fragile otoliths such as herring than for species with large, robust otoliths such as gadoids. For examples, Prime (1979) seldom recovered herring otoliths from captive harbour seals fed herring; Hawes (1983) recovered only 6% of the northern anchovy otoliths fed to sea lions; da Silva and Neilson (1985) recovered only 2 (4%) of the herring otoliths fed to harbour seals; and Murie and Lavigne (1985) found that herring otoliths were often digested while still in the stomach. In contrast, Prime (1979) recovered 87% of the gadoid otoliths fed harbour seals and McConnell *et al*. (1984) recovered >78% of the gadoid and mackerel otoliths fed grey seals. Pitcher (1980) also noted that scat analyses may not detect larger prey, most notably salmonids, because their heads (i.e. otoliths) may be discarded prior to being consumed, and cartilaginous fish, because they lack well-defined otoliths.

We contend that such biases can be minimized by utilizing, in conjunction with otoliths, many additional skeletal structures (Section 4.3; Appendix I). The improved resolution gained can be illustrated by examining the prevalence of prey in select collections in which they constituted the focal prey (i.e. prey that were far more prevalent in the collection than any other prey). Such collections for herring, hake and salmonids indicated that these prey were evident in almost all samples (Figure 8). For example, herring remnants were recovered in 86.4-100% ($\bar{x}$=96.1%; 150 of 156) of all samples (including those containing no identifiable prey) in collections where herring was the focal prey (Figure 8a). Thus, even if we assumed that all seals had consumed herring, their prevalence in the diet would only be underestimated by a factor of 1.04. Similarly, hake were present in 93.3-100% ($\bar{x}$=98.1%; 212 of 216) of all samples in collections where hake was the focal prey (Figure 8b); and salmonids in 73.8-90.0% ($\bar{x}$=77.7%; 73 of 94) of all samples in collections where salmonids were the focal prey (Figure 8c). Thus, even assuming all seals had consumed gadoids and salmonids, the prevalence of these prey would only have been underestimated by factors of 1.02 and 1.29 respectively.

The foregoing implied that remnants of each prey were found in most scats when they were consumed. The slightly lower proportion for salmonids probably did not indicate poorer resolution, but rather reflected the fact they did not predominate the diet to the same extent as herring and gadoids, as most samples without salmonids contained other prey. Based on the number and condition of elements recovered from other bony fishes, we surmise that they too were represented in almost all scats when they were consumed. For example, in some areas scats indicated that minuscule fishes, such as juvenile herring and sandlance, predominated the diet (e.g. Figure 21). It is worth noting, however, that even focal prey were not always represented by otoliths. For example, in the above collections, herring otoliths were found in only 62.7% of the samples containing herring, gadoid otoliths in 60.4% containing gadoids, and salmonid otoliths in 9.6% containing salmonids (Figure 8).

Although remnants of cartilaginous fishes were rarely found in harbour seal scats, we believe this indicated they were rarely consumed and not that they were completely digested. Using identical methods, spiny dogfish (*Squalus acanthias*), a small shark, was identified as the third most prevalent prey species in diet of sea lions (Olesiuk and Bigg 1988). We cannot dismiss the possibility that other soft-bodied prey had been consumed but not detected

in scat samples. However, the similarity in the diversity (Section 4.3) and mean number (Section 5.1c) of the prey identified in our scat samples and those reported in stomachs suggested that such biases, if they existed, were minimal.

e) All prey species comprising a meal had been consumed in equal quantities.

In equation [2], all prey species present in a sample were equally weighted, which assumed each had been consumed in equal quantities. Consequently, there would be a tendency to overestimate the importance of prey that comprised only a small portion of a meal, and underestimate the importance of prey that comprised the bulk of a meal.

Several other investigators have attempted to back-calculate the actual volume of prey consumed from the number and size of otoliths recovered from scats and otolith size - fish weight regressions (McConnell *et al.* 1984; Prime and Hammond 1987; Harvey 1989). We did not consider this procedure to be valid in the present study for several reasons. First, absolute meal volumes could not be established because our samples usually represented only portions of whole scats. Second, the relative volumes of prey in meals could not be reliably back-calculated due to the high degree of inter-specific (Figure 6) and intra-specific (i.e. a function of the size of prey) variation in otolith recovery rates. Third, we also found much intra-specific variation in the recovery rates of various structures (Section 4.3), such that estimates of the volume or the minimum numbers of prey would differ depending on the particular structures utilized, and otoliths alone could not be used since they were absent in many samples.

Although we were unable to derive or apply corrections to account for unequal volumes of prey being consumed, we assessed the maximum potential bias introduced by violations of the equal-volume assumption. An upper limit for the relative importance of a particular prey species was calculated by assuming that, in all samples in which the prey occurred, it comprised the entire meal and that all other prey species in the sample were consumed in negligible quantities. Conversely, lower limits were calculated by assuming that whenever the prey species occurred together with other prey that it had been consumed in negligible quantities. Mathematically, the upper and lower limits for the lth of $k=1,\ldots,n$ species were thus obtained by:

1) Setting $O_{kl}=1$ for $k=l$ and $O_{kl}=0$ for $k\neq l$

2) Setting $O_{kl}=0$ for $k=l$ and $O_{kl}=1$ for $k\neq l$

in equation [2], respectively.

For all but the two most predominant prey, hake and herring, the upper and lower limits provided relatively narrow ranges of their importance in the diet (Section 6.1). For example, the upper limits indicated that none constituted more than 10% of the overall diet, even if they had comprised the entire meal in all meals they were consumed. This was because they occurred in relatively few samples, or predation was highly localized (Sections 5.2 & 5.3). In other words, their overall contribution to the diet was small by virtue of their low prevalence, irrespective of the amounts consumed.

The validity of the assumption of equal volumes for the two most predominant prey, hake and herring, warranted closer examination for several reasons. First, these two species were by far the most prevalent, with hake present in 52.5% of all samples containing prey, herring in 57.8%, and both in 27.2%. As a result, the upper and lower limits for these species were wider, depending on the relative volumes of each consumed when both were present in the same meal. Second, the prevalence of these two species provided large sample sizes with which to conduct an *a posteriori* evaluation of the equal-volume assumption. Third, and most important, subjective observations of the relative abundance of the elements of each species in samples suggested that the assumption of equal volumes was in many cases violated. In some samples, the vast majority of elements were herring and only a few were hake. More often, however, samples contained many hake elements and only a few herring elements.

Since the recovery rates of hake and herring otoliths and other structures undoubtedly differed, it was not possible to calculate the absolute volumes of each species in samples. However, based on the numerical abundance of elements of each species in samples containing both, relative to the number of elements of each species in meals comprised exclusively of either one of the species, an index of their relative volumes in samples containing both was derived. Derivation of the volumetric index is described in detail in Appendix II.

In support of our subjective observations, the volumetric index indicated that one of the two species was generally predominant when both species were present (Figure 9). Hake predominated in 68.2% and herring in 31.9% of the samples containing both. Overall, the index indicated that hake comprised 77% and herring 23% of their total combined volume in samples containing both. To account for this bias, the volumetric index was incorporated as a weighting factor in equation [2]. If, for instance, the index indicated hake comprised 80% of and herring 20% of their combined volume in a sample, hake was scored as 1.6 and herring as 0.4, rather than each being scored as 1.

5.2 Diet within estuaries (Strait of Georgia)

Censuses indicated that the overall abundance of seals within estuaries was lowest during December-June, increased during July-August and peaked during September-November (Figures 10 & 11). Large numbers of scat samples (n=88-277; $\bar{x}$=164.8) were collected from estuaries in all months (Figure 3b).

Seasonal changes in diet composition for all estuaries combined are shown in Figure 12. Salmonids were consumed in all months ($\bar{x}$=10.3%), but were more prevalent during May-August (7.3-8.3%) and especially during September-January (14.5-21.2%). Predominant prey in estuaries were gadoids ($\bar{x}$=42.9%; 94.2% of which were hake) and to a lesser extent herring ($\bar{x}$=27.3%). Gadoids were the most prevalent prey (39.2-53.9%) in all months except February-March, during which herring was the most prevalent (49.5-50.6%).

Other important prey, which we defined as those constituting ≥1% of the overall diet or ≥2% of the diet in any given month, were plainfin midshipman ($\bar{x}$=3.6%), especially during May-June (9.7-10.5%); surfperches ($\bar{x}$=3.6%; 91.9% of which were shiner perch), flatfishes ($\bar{x}$=2.8%), and sculpins ($\bar{x}$=2.6%), all 3 of which were most prevalent during August-September (5.4-6.1%, 5.0-6.3% and 7.8-7.9% respectively); and cephalopods ($\bar{x}$=2.3%), especially during November-March (2.9-5.5%).

Incidental prey species included, in decreasing order of importance, rockfishes, sandlance, sticklebacks, hexagrammids, skates, northern anchovy, eelpouts, smelts, crabs, pricklebacks/gunnels, unidentified invertebrates (Species 'N'), shrimp, lamprey, birds and mussels. Unidentified prey accounted for a mean of 1.0% of the total diet.

Comox Harbour: The number of seals in Comox Harbour fluctuated between about 50-250 during December-July, subsequently increased during August-September, and peaked at approximately 475 in late October (Figure 11a). Large numbers of scat samples (n=55-146; $\bar{x}$=95.7) were collected from this estuary in all months.

Seasonal changes in diet composition in Comox Harbour (Figure 13) resembled those observed in all estuaries, but the seasonal changes were more pronounced. Salmonids were consumed in all months ($\bar{x}$=19.9%), but mainly during May-September (14.8-18.1%) with a definite peak during October-December (30.4-42.3%). Smolt-sized salmonids, tentatively identified as *Salmo* spp. (Section 6.3), accounted for 36.8-39.4% of the salmonids consumed during May-June, 9.7-10.8% of those consumed during July-August, and 2.5-5.2% of those consumed in September-October. The autumn peak in salmonid predation (Figure 12) coincided with the influx of seals into the estuary (Figure 13a).

In addition to salmonids, the diet was predominated by herring ($\bar{x}$=34.4%) and gadoids ($\bar{x}$=24.0%; 94.2% hake with the remainder being tomcod and Pacific cod). Herring was the predominant prey during January-April (49.3-75.8%) and gadoids during May-September (19.8-46.3%). Other important prey included flatfishes ($\bar{x}$=5.0%), sculpins ($\bar{x}$=4.8%), plainfin midshipman ($\bar{x}$=4.5%) and surfperches (2.9%; 85.8% shiner perch and 14.2% pile perch). As in all estuaries combined, plainfin midshipman were most prevalent during May-June (14.3-15.3%), and flatfishes and sculpins during August-September (8.9-12.4% and 9.8-13.8% respectively). Incidental prey species included, in decreasing order of importance, cephalopods, rockfishes, skates, crabs, hexagrammids, sticklebacks, eelpouts, pricklebacks, shrimp, smelts, gunnels and sea urchins. A mean of 1.4%

of the diet was comprised of unidentified prey.

Mud-Fanny-Deep Bays: Seasonal trends in seal abundance were similar in each of these estuaries in that numbers peaked during January-March but subsequently declined to very low levels by May-December (Figure 11b). However, a secondary peak in abundance occurred in Mud Bay only during September-November. Scat samples were collected intermittently from this area. Nineteen samples, 12 from Mud Bay and 7 from Fanny Bay, were collected during peak abundance in February-March; 2 small collections totalling 12 samples were collected from Mud Bay during lowest abundance in May-June; and 30 scats were collected from Mud Bay during the autumn peak in November-December.

The diet in both Mud and Fanny Bays during February-March, which coincided with the large influx of seals, was comprised almost exclusively of herring (88.7%) along with some shiner perch (11.4%)(Figure 14). The waters adjacent to these estuaries are an important herring spawning ground (R.W. Armstrong, Nanaimo, B.C., pers. comm.) and, judging from the tremendous bird activity observed during the March aerial census, spawning appeared to have been underway at the time.

In May-June, when fewer seals were present, the diet was not predominated by any prey species (Figure 14). Salmonids comprised only 2.9% of the total diet. Other important prey included plainfin midshipman (31.5%), herring (29.2%) and flatfishes (20.2%). In contrast to most estuaries, gadoids (unidentified but none of which were hake) constituted only 2.9% of the diet. Incidental prey included surfperches and cephalopods, and unidentified prey accounted for 9.8% of the diet.

In November-December, coinciding with the secondary influx of seals into Mud Bay, the prevalence of salmonids increased to 9.6% of the diet (Figure 14). Other important prey species, none of which predominated, were flatfishes (22.5%), herring (16.4%), rockfishes (15.2%), sandlance (11.2%), sculpins (4.3%; primarily staghorn sculpins), and cephalopods (3.4%; including at least one octopus). As in previous months, gadoids (unidentified but not hake) were a relatively minor (2.5%) dietary item. Incidental prey included, in decreasing order of importance, plainfin midshipman, surfperches, and crabs. Unidentified prey accounted for 7.6% of the diet.

Nanaimo River: The number of seals in the Nanaimo River estuary fluctuated between approximately 20-100 during December-August, but subsequently increased during September and peaked at about 150 in October (Figure 11c). Fairly large numbers of scat samples were collected in all months except May-July. Four collections totalling 72 samples were collected during January-April and five totalling 90 samples were collected during August-December.

Seasonal changes in diet in the Nanaimo River estuary (Figure 15) resembled those in all estuaries (Figure 12). Salmonids were a minor dietary item during January-April (2.2-2.8%) but, again coinciding with the fall influx

of seals, increased to 17.8-22.5% of the diet during August-November. As in most other estuaries, herring predominated the diet during November-April (60.9-75.8%), and gadoids during August-September (60.7-64.5%; 95.9% of which were hake and the remainder walleye pollock and tomcod) and presumably during the months no samples were collected. Other important prey included cephalopods, especially during February-March (9.5-16.0%), and plainfin midshipman. Incidental prey included, in decreasing order of importance, shiner perch, lamprey, lingcod, birds, and sculpins. Unidentified prey accounted for a mean of 0.3% of the diet.

Shoal Islets: Few seals inhabited the Shoal Islets estuary during December-February, but numbers steadily increased to a peak of about 225 by October (Figure 11d). Except for January, fairly large numbers of scat samples were collected from this estuary in all months (n=19-138; $\bar{x}$=88.5).

Seasonal changes in diet composition in the Shoal Islets are shown in Figure 16. Salmonids constituted a negligible portion of the diet (0-0.9%) during February-September. Although there was a substantial influx of seals during October-November, the prevalence of salmonids in the diet increased only marginally to 1.5-1.6%. The scarcity of salmonids cannot be attributed to small sample sizes or to annual variations, as the sample-sizes for October-December were large (n=34-115; $\bar{x}$=76.7) and were obtained in 1986, 1987 and 1988.

As in most estuaries, the diet was predominated by gadoids (52.7-78.4%; 96.5% hake and the remainder walleye pollock, tomcod and Pacific cod), and to a lesser extent by herring (16.5-41.1%). However, the seasonal shift between these two species observed in most estuaries was not evident. Other important prey included cephalopods ($\bar{x}$=2.5%), mainly in November-May; plainfin midshipman (2.0%), mainly in April-June; surfperches (2.0%; 88.7% shiner perch and 11.2% pile perch), mainly in February-March, and gunnels in September ($\bar{x}$=0.5%). Incidental prey species included, in decreasing order of importance, rockfishes, lingcod, flatfishes, sandlance, crabs, northern anchovy and sticklebacks. Unidentified prey only accounted for a mean of 0.1% of the total diet.

Cowichan Bay: The number of seals in Cowichan Bay gradually increased from a low of about 30 in April to a peak of about 100 by December (Figure 11e). Scat samples were collected in all months of the year, though sample sizes were small for some months (n=15-88; $\bar{x}$=40.7).

Seasonal changes in the diet in Cowichan Bay (Figure 17) resembled those observed in all estuaries, but fluctuations were again more pronounced. Salmonids were consumed in all months except May ($\bar{x}$=15.6%), but primarily during October-January (23.6-48.5%). As in most estuaries, the increase in salmonid predation in fall-early winter (Figure 17) coincided with the influx of seals into the estuary (Figure 13e).

In addition to salmonids, the diet was predominated by herring ($\bar{x}$=34.4%) and gadoids ($\bar{x}$=29.8%; 84.0% hake and the remainder walleye pollock, Pacific cod and tomcod). The seasonal shift between these two prey evident in

most estuaries was not apparent in this estuary. Other important prey were surfperches ($\bar{x}$=5.2%; 89.1% shiner perch, 6.7% pile perch and 4.2% an unidentified species) especially during February-April (4.1-9.3%) and August-November (4.7-12.4%); cephalopods ($\bar{x}$=3.3%) particularly during December-March (5.9-11.1%); sculpins ($\bar{x}$=2.8%); flatfishes ($\bar{x}$=1.8%) especially during August-September (7.1-7.7%); sticklebacks ($\bar{x}$=1.7%) during April-July; plainfin midshipman ($\bar{x}$=1.6%) particularly during May-June (4.4-5.8%); and rockfishes ($\bar{x}$=1.0%) especially during October-November (4.3-4.9%). Incidental prey included, in decreasing order of importance, eulachon, birds, sandlance, hexagrammids, unidentified invertebrates (Species 'N'), unidentified crustaceans and northern anchovy. Unidentified prey accounted for a mean of 1.5% of the diet.

Mill Bay: About 60 seals inhabited Mill Bay throughout the year (Figure 11f). Scats were collected from this estuary in all months, but sample sizes during February-August tended to be smaller (n=6-25, $\bar{x}$=14.9) than those during September-January (n=47-175; $\bar{x}$=91.6).

Seasonal changes in the diet in Mill Bay are shown in Figure 18. Predation on salmonids was undetectable during February-August, and increased only marginally to 1.5-7.1% of the diet during September-January. As in estuaries in general, the diet was predominated by gadoids (37.3-82.6%; 98.6% hake and the remainder tomcod) and, to a lesser extent, by herring (7.1-58.0%). It should be noted that the apparent oscillations between these two prey during February-June may have been an artefact due to the small sample-sizes for these months.

Other important prey species included rockfish ($\bar{x}$=3.6%), especially in June; plainfin midshipman ($\bar{x}$=2.3%) during November-February; sculpins ($\bar{x}$=1.7%) especially during July-August; shiner perch ($\bar{x}$=1.6%); cephalopods ($\bar{x}$=1.0%) during October-January, gunnels ($\bar{x}$=0.8%) in August; and lingcod (0.4%) in December-February. Incidental prey species included, in decreasing order of importance, flatfishes, shrimp, sticklebacks, sandlance, northern anchovy, smelts, crabs, eelpouts, and ronquills. Unidentified prey items accounted for only 0.1% of the total diet.

Squamish River: The Squamish River estuary was not routinely censused with other estuaries. During two aerial censuses of this estuary in August and September, we observed only 0 and 2 seals respectively. According to local sources, numbers increased to very roughly 40-50 by October-November (C. Tamburri, Squamish, B.C., pers. comm.). The trends illustrated in Figure 11c should thus be considered as tentative.

Only one scat collection was made in this estuary. It was obtained in June and was comprised of 9 samples. All 9 samples contained hake and one also contained a few herring elements which, when volumetrically weighted, indicated that the diet was comprised of 96.4% hake and 3.3% herring.

Port Moody: Port Moody was also not routinely censused with other estuaries. Boat counts by us and local residents (R. McVicar, Port Moody, B.C., pers. comm.) suggested that, very crudely, numbers were low (50-75) during April-July, but subsequently increased to a peak of 160 by October. Scats were collected only intermittently from this estuary and sample sizes were often small: 17 samples during March-April; 13 during June-July; and 34 during September-December.

The diet composition for Port Moody is shown in Figure 19. Salmonids comprised 8.5-9.7% of the diet during March-April, 2.4% during June-July, and 9.8-16.0% during September-December. Of the salmonids taken in September-October, 46.5 and 37.1% respectively were juvenile-sized fish tentatively identified as *Salmo* spp (see Section 6.3).

As in most other estuaries, the diet was predominated by gadoids (18.4-53.2%) and herring (16.3-50.0%). Hake, which accounted for only 55.9% of all gadoids, did not dominate the gadoids to the same extent as in most other estuaries. Instead, walleye pollock (25.3%) and Pacific cod (18.8%) also comprised appreciable proportions of the gadoids.

Other important prey species were plainfin midshipman ($\bar{x}$=6.3%) during June-July; sculpins ($\bar{x}$=5.1%; mainly *Oligocottus* spp.); surfperches ($\bar{x}$=5.1%; 79.4% shiner perch and 20.6% pile perch) during March-April; cephalopods ($\bar{x}$=2.2%); sticklebacks ($\bar{x}$=1.7%); flatfishes ($\bar{x}$=1.0%); and smelts ($\bar{x}$=0.9%). Incidental prey species included, in decreasing order of importance, lamprey, northern anchovy, greenlings, skate, shrimp, crabs and rockfishes. Unidentified prey accounted for an average of only 0.3% of the overall diet.

Boundary Bay - Fraser River: By far the largest numbers of seals in estuaries occurred in Boundary Bay and the mouth of the Fraser River (Figure 10). Aerial censuses indicated that Boundary Bay was apparently vacated during December-March, numbers subsequently increased during April-July, peaked at approximately 900 in August, and then declined. The seasonal peak occurred several months earlier than in most other estuaries and coincided with the pupping season. This may indicate that the estuary was a preferred whelping area similar to other estuaries along the coast of Washington and Oregon (Jefferies 1986). The abandonment of this estuary in late autumn-winter may have been related to the seals preference to haul out during daylight, as the sandbars used as haulouts were only exposed at night during the late autumn and winter. Seasonal trends in abundance at the mouth of the Fraser River followed a similar pattern except that, typical of most estuaries, peak abundance of 1,100 occurred in September. The increase between August and September probably represented immigration from Boundary Bay, as the combined counts for the two estuaries in August and September were more stable than the individual counts.

Scat samples were difficult to obtain from these areas, especially from Boundary Bay, as the sandbars used as haulouts were exposed for only a few hours during each tidal cycle. Five collections, totalling 63 samples, were obtained from Boundary Bay during June-August, the period of peak abundance; and one collection of 22 samples from the Fraser River in late September, also the

period of peak abundance.

Seasonal changes in the diet for Boundary Bay and Fraser River combined are shown in Figure 20. Salmonids were preyed upon in all months ($\bar{x}$=21.9%), and were by far the predominant prey (65.6%) during September-October, which coincided with peak seal abundance at the mouth of the Fraser River. In addition, the diet was predominated by surfperches ($\bar{x}$=25.7%; 97.9% shiner perch and 2.1% pile perch) and gadoids ($\bar{x}$=20.7%; 73.3% hake with the remainder unidentified, but not hake). Other important prey included sculpins ($\bar{x}$=11.1%), especially during July-September (9.9-26.8%); and flatfishes ($\bar{x}$=10.5%), especially during June-September (7.4-22.0%). In contrast to most estuaries, herring comprised only a negligible portion of the diet ($\bar{x}$=2.7%), which was probably due to the fact that few seals inhabited this area when herring were typically the predominant prey.

Incidental prey included, in decreasing order of importance, crabs, cephalopods, smelts, plainfin midshipman and lamprey. Unidentified prey accounted for a mean of 2.4% of the diet.

5.3 Diet outside estuaries (Strait of Georgia)

During the entire year, the vast majority (83-95%; $\bar{x}$=89.7%) of seals resided outside estuaries (Figure 21). Fairly large numbers of scat samples (n=29-146; $\bar{x}$=71.9) were collected outside estuaries in all months (Figure 3b).

Seasonal changes in the diet for all non-estuary sites combined are shown in Figure 22. Salmonids comprised a relatively minor part (0-5.2%; $\bar{x}$=3.1%) of the diet in all months. As in estuaries, but not nearly to the same extent, salmonid predation increased through June-September and peaked during October-November. The non-estuary diet was predominated by gadoids ($\bar{x}$=45.7%; 94.5% of which were hake and the remainder tomcod, walleye pollock and Pacific cod) and herring ($\bar{x}$=33.0%). As in most estuaries, there was a distinct seasonal shift in the importance of these prey, with gadoids dominating during April-October (54.3-73.7%) and herring during December-March (58.0-70.2%).

Other important prey were hexagrammids ($\bar{x}$=3.4%; 95.8% lingcod and 4.2% greenling), especially during December-April; plainfin midshipman ($\bar{x}$=3.4%), especially during April-June and November-December; surfperches ($\bar{x}$=2.2%; 81.3% shiner perch and 18.7% pile perch); cephalopods (2.1%); and sandlance (0.9%). Incidental prey species included, in decreasing order of importance, rockfishes, flatfishes, sculpins, smelts, skates, gunnels, lamprey, pricklebacks, crabs, sticklebacks, clingfishes, eelpouts and sea urchins. Unidentified prey accounted for a mean of 2.0% of the total diet.

Northern Gulf: Extrapolations from censuses conducted between late May and October suggested that a mean of 48.8% of the total non-estuary popu-

lation resided in the Northern Gulf (Figure 21). Since the seasonal changes in distribution were based on extrapolations rather than actual counts, we did not attempt to correlate shifts in diet with changes in abundance. Scats were collected from the Northern Gulf in all months except September and October. Collections in most months sampled were fairly large (n=23-110; $\bar{x}$=52.4) with the exception of May (n=3) and November (n=11).

Seasonal changes in diet composition for all sites within the Northern Gulf (Figure 23) resembled those of the all non-estuary sites combined (Figure 22). Salmonids were consumed in most months ($\bar{x}$=2.7%) but were most prevalent during July-August (7.1-11.3%). Although no samples were collected during September-October, the prevalence of salmonids had declined to 0-1.8% by November-December. Thus, salmon predation in this region appeared to peak earlier than in estuaries and other regions of the Strait of Georgia.

As in the Gulf in general, gadoids ($\bar{x}$=47.8%; 97.6% and the remainder walleye pollock and Pacific cod) and herring ($\bar{x}$=24.4%) predominated the diet. The seasonal shift between the two prey was similar to the entire Gulf, but herring were not as predominant during November-March as in other regions. Instead, hexagrammids (99.0% lingcod and 1.0% greenling) formed a major part of the diet (16.0-29.3%) in these months. Other important prey were rockfishes ($\bar{x}$=3.0%), mainly during November-April; surfperches ($\bar{x}$=2.5%; 75.6% shiner perch and 24.4% pile perch); and cephalopods ($\bar{x}$=1.8%). Incidental prey species included, in decreasing order of importance, plainfin midshipman, flatfishes, sculpins, sea urchins, sandlance, and penpoint gunnels. Unidentified prey items accounted for a mean of 4.0% of the total diet.

Gulf Islands: Based on extrapolations from censuses conducted between late May and October, we estimated that a mean of 29.4% of the total non-estuary population resided in the Gulf Islands (Figure 21). Because the seasonal changes in distribution were based on extrapolations rather than actual counts, we did not attempt to correlate variations in diet with changes in abundance. Scat collections from Gulf Island sites were large in all months (n=50-153; $\bar{x}$=100.9).

Seasonal changes in diet within the Gulf Islands (Figure 24) were similar to those for all non-estuary sites combined (Figure 22). Salmonids constituted a mean of 3.1% of the overall diet, were more prevalent (2.3-3.6%) during June-October, and most prevalent (6.7-8.1%) during November-December. Of the 14.5% of salmonids consumed in November-December that could be keyed to species, all were chum salmon.

As in the Northern Gulf, gadoids ($\bar{x}$=47.1%; 94.2% of which were hake and the remainder tomcod, walleye pollock, and Pacific cod) and herring ($\bar{x}$=34.3%) were the two predominant prey. Gadoids predominated (58.4-74.8%) during April-October and herring (56.4-70.3%) during December-March.

Other important prey were plainfin midshipman ($\bar{x}$=4.7%), particularly during April-June (5.6-10.4%) and during November-December (10.2-11.1%); cephalopods ($\bar{x}$=2.5%); surfperches ($\bar{x}$=2.1%; 85.9% shiner perch and 14.1% pile perch);

and hexagrammids ($\bar{x}$=1.2%; 85.5% lingcod and 14.5% greenlings), especially during March-April (3.5-6.2%). Incidental prey species included, in decreasing order of importance, flatfishes, sculpins, smelts, rockfishes, skates, sandlance, gunnels, lamprey, sticklebacks, crabs, eelpouts and pricklebacks. Unidentified prey items accounted for a mean of 1.3% of the total diet.

Southern Gulf: Based on extrapolations of censuses conducted between late May and October, we estimated that a mean of 21.8% of the total non-estuary population resided in the Southern Gulf (Figure 21). Because the seasonal changes in distribution were based on extrapolations rather than actual censuses, we did not attempt to correlate shifts in diet with changes in abundance. Scat samples were collected in the Southern Gulf in all months except January, though sample sizes were small for some months. Since only 1-3 ($\bar{x}$=2.3) samples were collected in each of February, March and April, and July, no attempt was made to estimate the diet in these months. Collections in the remaining 7 months ranged from 9-31 ($\bar{x}$=19.6).

The limited data available for the Southern Gulf suggested that the diet in this region (Figure 25) was distinctly different from the diet in other non-estuary regions (Figures 22 and 23). During May-June, gadoids were a fairly predominant prey, but comprised only 15.8-26.9% of the diet, compared to 58.5-63.4% in the Gulf Islands and 64.3-72.6% in the Northern Gulf during the same period. Also, the gadoids in the Southern Gulf were dominated to a lesser extent (76.6% hake and the remainder unidentified but not hake) than in other non-estuary regions. The two other predominant prey were herring (36.9-40.1%), which unlike other non-estuary regions were predominately juvenile, and sandlance (31.6-38.3%), which had not previously been a predominant prey. Other important prey were sculpins (1.5-1.9%, primarily *Oligocottus* spp.) and flatfishes (1.4-1.9%).

By August, gadoids still comprised an atypically small portion of the diet (20.4%) and sandlance continued to be a predominant prey (24.4%). However, herring disappeared from the diet and was replaced by a wide variety of other species: sculpins (13.3%; 43.4% of which were great sculpins, 34.8% staghorn sculpins and 21.7% buffalo sculpins), eulachon (9.6%), starry flounder (7.5%), rockfish (5.8%), lingcod (5.3%), and skate (2.3%). Unidentified prey accounted for 11.4% of the total diet.

By September-October, the diversity of the diet had decreased markedly. The prevalence of salmonids, which were absent in previous months, increased to 3.7-5.1% of the diet. Both gadoids (20.4-45.9%; 90.4% hake and 9.6% tomcod) and herring (30.4-49.4%) also increased in importance.

During November-December, as in other non-estuary regions, the diet was predominated by herring (79.2-81.0%). Other important prey were sculpins (3.8-4.0%; 85.8-85.9 of which were staghorn and the remainder buffalo sculpins), salmonids (1.6-1.7%), shiner perch (1.6-1.7%), cephalopods (1.6-1.76%), rockfishes (1.1-1.2%) pricklebacks (1.1-1.2%) and gunnels (1.1-1.2%). Incidental prey included clingfishes, rex sole and skates.

5.4 Diet in other regions

Masset Inlet: The Masset Inlet harbour seal population, censused in July 1986, was estimated at approximately 400 seals. Thirty-four scat samples were collected in April and 7 in June, 1983, from 4 sites distributed throughout Masset Inlet.

In April, seals consumed a wide variety of prey, none of which accounted for more than 30% of the diet (Figure 26). Salmonids constituted only 0.8% of the diet. Predominant prey were herring (30.0%), flatfishes (17.1%; mainly starry flounder), shiner perch (11.0%), sandlance (10.5%), sculpins (10.1%), and gadoids (7.9%; unidentified but not hake). Unidentified prey accounted for 3.6% of the total diet. The few samples collected in June indicated that herring had become by far the most predominant (75.3%). Other important prey included flatfishes (14.3%), rockfishes (5.2%), and sculpins (5.2%). Incidental prey in either or both months included skate, sticklebacks, shrimp, unidentified invertebrates (Species 'N'), eelpouts, cephalopods and smelts.

Western Vancouver Island: Aerial censuses conducted in 1987 indicated the seal population off southwestern Vancouver Island numbered approximately 550 and that in Barkley Sound about 600. Censuses have not yet been conducted north of Barkley Sound. Twenty-three small collections (courtesy of H. Reisenleiter), totalling 58 samples, were collected from 4 sites distributed along the southwest coast of Vancouver Island (Figure 2) during July-October, 1988-89; one sample was collected from Barkley Sound (Figure 2) in June, 1987; and one collection of 10 samples was made from Gull Islet off the northwest coast of Vancouver Island (Figure 1) in February, 1988.

The diet off southwestern Vancouver Island during July-October (Figure 26) was similar to that in the Strait of Georgia during the same period. Salmonids comprised a minor part (0.3-3.0%) of the diet, which was predominated (50.0-60.0%) by gadoids (98.8% hake with the remainder tomcod) and to a lesser extent (11.4-27.9%) by clupeids (86.9% of which were herring and 13.2% American shad). Other important prey were hexagrammids ($\bar{x}$=6.2%; 62.1% of which were lingcod and 37.9% greenlings), rockfishes ($\bar{x}$=6.0%), cephalopods ($\bar{x}$=2.9%), surfperches (2.2%), sandlance (1.7%), and flatfishes (1.6%). Incidental prey included sculpins (mainly *Oligocottus* spp.), smelts, gunnels and crabs. Unidentified prey species accounted for a mean of 3.6% of the total diet.

The single scat collected in Barkley Sound contained only rockfish.

The diet off northwestern Vancouver Island in February (Figure 26) was comprised mainly of herring (34.1%) and lingcod (33.2%). Other important prey species were gadoids (9.1%; primarily hake), smelts (5.6%), cephalopods (5.3%) and pileperch (5.3%). Salmonids comprised 4.2% of the diet and unidentified prey 3.3% of the diet.

Johnstone Strait: Censuses have not been conducted in Johnstone Strait, but censuses conducted in the adjacent Queen Charlotte Strait in 1988 indicated that the density of seals was about 38% that of the Strait of Georgia. Thirty scats were collected from one site in July, 1988, and 19 samples from two sites in September, 1988.

The diet in both July and September was predominated by salmonids (30.1-30.2%) and herring (34.8-40.9%). In contrast to non-estuary sites in the Strait of Georgia during this period, gadoids (primarily walleye pollock) comprised only 4.2-5.1% of the diet. Other important prey were smelts ($\bar{x}$=11.2%; mainly eulachon) in July, flatfishes ($\bar{x}$=3.3%), cephalopods ($\bar{x}$=2.4%) and shiner perch ($\bar{x}$=3.4%). Incidental prey included, in declining order of importance, skates, rockfishes, sculpins (mainly *Oligocottus* spp.), plainfin midshipman, greenlings and wolfeel. Unidentified prey accounted for a mean of 2.4% of the diet.

6. PREY CONSUMPTION

6.1 Annual food requirements

Seasonal fluctuations in the estimated total size of the Strait of Georgia seal population as a result of mortality and recruitment are illustrated in Figure 21. The population declined throughout most of the year as a result of mortality, except during the July-August pupping season when recruitment exceeded mortality. As a result, the population increased from its minimum of 12,990 just prior to the pupping season (18 June) to a peak of 15,810 toward the end of the pupping season (6 September), with a mean population size of 14,270. Note that because the population was below its carrying capacity and increasing at its intrinsic rate of 12.5% per annum (Olesiuk *et al.* in press), the population was 12.5% larger at the end than at the beginning of the year.

The estimated proportion of the Strait of Georgia population inhabiting estuaries varied from a minimum of 5% in late winter (January-March) to a maximum of 17% in fall (September-October) (Figure 21). Weighted seasonally, an average of 10.3% of the population resided in estuaries.

Mean per capita food requirements, weighted according to the sex- and age-structure of the population and the mean energetic density of prey, was estimated at 1.9 kg·day^{-1} (Olesiuk *et al.*, in prep.). Total annual prey consumption in 1988 was therefore estimated at 9,895 tonnes (1,023 tonnes in estuaries and 8,870 tonnes outside estuaries).

6.2 Annual prey consumption

The estimated annual consumption rates of prey in the Strait of Georgia, based on the low-level stratification (i.e. all estuaries pooled and all non-estuary sites pooled) are shown in Figure 27. The most important prey, both within and outside estuaries, and thus overall, was gadoids. Total annual gadoid consumption was estimated at 4,466.9 tonnes, 453.8 tonnes within and 4,013.1 outside estuaries (Table 4). The gadoids consumed were 94% hake both within and outside estuaries. The second most predominant prey, again both in and outside estuaries, and thus overall, was herring. Total annual herring consumption was estimated to be 3,206.3 tonnes, 244.2 in and 2,962.1 tonnes outside of estuaries respectively (Table 4).

Salmonids were the third most important prey overall (Figure 27). They ranked third in importance in estuaries (11.4%) and fifth outside estuaries (3.2%). Total annual salmonid consumption was estimated at 397.7 tonnes, of which 117.4 tonnes was consumed within and 280.3 tonnes outside of estuaries respectively (Table 4). Plainfin midshipman, which ranked sixth in importance within estuaries and fourth outside estuaries, was fourth in importance overall. Total annual plainfin midshipman consumption was estimated at 33.5 and 301.9 tonnes within and outside estuaries respectively, for a total of 335.4 tonnes. Hexagrammids, which constituted a negligible portion of the diet within estuaries (0.3%) but ranked third in importance outside estuaries (3.5%), ranked fifth overall. Annual hexagrammid consumption was estimated at 310.8 tonnes, 308.1 of which was consumed outside of estuaries. Other important prey in the overall diet were surfperches (2.3%), cephalopods (2.1%), flatfishes (1.2%), sculpins (1.2%) and rockfishes (1.1%). All other prey combined, none of which comprised more than 1% of the diet, accounted for 2.1% of the overall diet and unidentified prey for 1.8% of the overall diet.

Despite the differences in diet between estuaries and among non-estuary regions (Sections 5.2 and 5.3), further stratification by individual estuary and non-estuary region (i.e. high-level stratification) had little effect on the consumption estimates cited above. In comparing the high- and low-level estimates, we eliminated all prey that constituted <1% of the diet by either scheme. Otherwise, the correlation between the two would have been inflated owing to the large number of incidental prey species that comprised negligible proportions of the diet in according to both schemes. There was a high degree of concordance between the low- and high-level estimates both in absolute terms (r^2=0.996 on an arithmetic scale) and relative terms (r^2=0.879 on a log-log scale; Figure 28).

The similarity of the low-level and high-level estimates indicated that any inaccuracies introduced in the former by the pooling of dissimilar estuaries and non-estuary regions were relatively minor. In other words, the samples collected from estuaries seemed to be representative of estuaries in general and the samples collected outside estuaries of non-estuary sites in general. As noted earlier, the low-level estimates were more precise as they were based on larger sample sizes. We therefore accepted the low-level estimates as the best estimates of total annual prey consumption.

Although the high-level estimates were considered to be inferior, they were used to partition prey consumption among individual estuaries and non-estuary regions (Table 4). It should be noted that, as a result of this procedure, the estimates of prey consumption for individual estuaries and non-estuary regions do not exactly sum to the total estimates for all estuaries and non-estuary sites combined (Table 4). For example, the total consumption of hexagrammids in individual estuaries and non-estuary regions add up to 457.7 tonnes, whereas the total estimated consumption for all estuaries and non-estuary regions combined was only 310.8 tonnes. The discrepancy can largely be attributed to the high estimate for the Northern Gulf, which was less reliable as it was based on relatively small numbers of samples obtained from only a few sites (see Hexagrammids; Section 6.3).

As noted earlier (Section 5.1e), the accuracy of the consumption estimates were contingent upon the unverifiable assumption that all prey comprising a meal had been consumed in equal quantities. The potential range of uncertainty in the estimates due to possible deviations from this assumption are given in Table 6. As outlined in Section 5.1e, the upper and lower estimates were calculated for each prey by assuming it had comprised the entire or a negligible portion of all meals that also contained other prey. Thus, the upper and lower estimates are not probabilistic, but rather extreme limits. Since it was highly unlikely that a particular prey always comprised entire or a negligible portion of mixed meals, the actual consumption rates undoubtedly lie toward the middle of these limits. On the other hand, additional error in the prey consumption estimates may arise as a result of inaccuracies in the estimated mean per capita daily food requirement, which may potentially vary by ±30-40% of the point estimate (see Olesiuk in prep.). Since the above biases tend to cancel, the calculated limits probably crudely reflected the true uncertainty in annual prey consumption.

The calculated lower and upper limits typically ranged from 35-211% of the point estimates (Table 5). For example, they indicated that annual salmonid consumption might potentially be as low as 124.5 tonnes or as high as 848.3 tonnes, or 31% and 213% of the point estimate of 397.7 tonnes. Although the ranges for gadoids and herring were narrower in relative terms (62-135% and 61-169% respectively), they were much wider in absolute terms (+/- 1563.5/ 1693.6 and +/- 2203.2/1250.9 tonnes respectively) than those of other prey. Because the point estimates for the latter two prey had been volumetrically-weighted (Appendix II), the actual consumption was more likely to fall toward the middle of the range than for other species. Species that rarely comprised an entire meal, such as sculpins and cephalopods, had the lowest lower limits. Conversely, because these species were usually consumed together with many others in the same meal, they also tended to have the highest upper limits.

Although often wide, the limits were nevertheless useful for assessing the importance of prey. For example, the limits for gadoids and herring indicated that these species combined accounted for, at minimum, almost half (47.8%) the overall diet. Indeed, subsequent calculations indicated that these two prey accounted for at least 63.2% of the total diet, as in many cases they were the only two prey in a meal such that both could not have been consumed in negligible quantities. The upper limits also indicated that all other prey each accounted for less than 10% of overall diet, and only 5 (salmonids, plainfin

midshipman, hexagrammids, surfperches, and cephalopods) could have accounted for more than 5% of the overall diet.

6.3 Significance and patterns of seal predation

To this point, only the importance of prey species from the seals' perspective (i.e. the contribution of each prey to the annual food requirements) has been considered. In this Section, we assess the importance from other perspectives by comparing the estimated annual consumption to the size of fish stocks, sport and commercial catches, and the seasonal and regional availability of each prey. The discussion is directed toward the 5 most important prey, each of which accounted for >3% of the total prey consumed, and combined accounted for 88.0% of the total prey consumed.

Gadoids: Total annual consumption of gadoids in the Strait of Georgia study area was estimated at 4467 tonnes (range 2773-6030 tonnes), which was comprised of an estimated 4214 tonnes of hake, 101 tonnes of tomcod, 97 tonnes of walleye pollock and 54 tonnes of Pacific cod. Since none of the latter 3 species accounted for ≥1.0% of the diet, the following discussion focuses on hake.

The Pacific hake in the Strait of Georgia comprise a distinct, non-migratory population and are the most abundant resident fish in the area (Beamish *et al.* 1982; McFarlane and Beamish 1985; Shaw *et al.* in press). Trawl surveys have indicated that the total biomass of this stock is on the order of 110-125,000 tonnes (Shaw *et al.* in press). Saunders and Shaw (1989) estimated the stock could sustain an annual harvest of 11,000 tonnes with average recruitment, but the stock is presently under-utilized. The Strait of Georgia hake fishery only began in 1979-80, during which period catches were on the order of 500 tonnes. In subsequent years, catches have generally increased and in recent years (1984-88) have ranged from 5-9,000 ($\bar{x}$=5,950) tonnes (Saunders and Shaw 1989). The annual biomass consumed by seals therefore represents about 3.5% (range 2.0-5.2%) of the total standing stock, or about 71% (range 47-101%) of the recent mean commercial harvest.

The seasonal and regional patterns of seal predation on hake outside estuaries (Figures 22-25), where 90% of hake predation occurred (Table 5), appear to reflect the seasonal availability of this prey. During March-April, hake concentrate in dense spawning aggregations in the open waters of south central Strait of Georgia (see Figure 4 in McFarlane and Beamish 1985). During this time, the main body of fish occurs at depths of 150-300 meters. Thus, hake may be too deep and far offshore to be readily available to harbour seals, which would explain their scarcity in the diet at this time. Once spawning is concluded in late April-early May, post-spawning hake disperse along the east side of Vancouver Island toward the northern stretches of the Strait of Georgia. During this period, hake form schools in shallower waters of 50-80 meters during the day and become widely dispersed in the upper 100 meters at night (McFarlane

and Beamish 1985). Coinciding with the post-spawning dispersal, hake consumption increased in the Gulf Islands and Northern Gulf and hake remained the predominant prey until November (Figures 23 and 24). By December, hake are relatively scarce in the Strait of Georgia and it is suspected that they have dispersed north into Johnstone Strait (McFarlane and Beamish 1985) or up mainland inlets (B. Shaw, Nanaimo, B.C, pers. comm.). This coincided with a sharp decline in the prevalence of hake in both the Gulf Islands and Northern Gulf (Figures 23 and 24). The prevalence of hake may also have been attenuated by the greater availability of herring in December (see below). The relative unimportance of hake in the diet in the Southern Gulf (Figure 25) can be attributed to the fact that the post-spawning migration of hake is generally northwards.

The seasonal pattern of seal predation on hake within estuaries was similar to that outside of estuaries, but not nearly as pronounced (Figure 12). However, closer examination of individual estuaries indicated that in some, such as Comox Harbour and the Nanaimo River estuary (Figures 13 and 15), the seasonal shifts were virtually the same as those outside of estuaries, whereas in others, such as the Shoal Islets and Mill Bay (Figures 16 and 18), hake continued to be the main prey species throughout the year. The latter might reflect predation on small localized stocks of hake, which are known to reside in some inlets, including Saanich Inlet adjacent to Mill Bay (G. McFarlane, Nanaimo, B.C, pers. comm.). Alternatively, seals in the latter estuaries may have been targeting juvenile hake, which are widely distributed in shallow water throughout the Strait in all months, but we have not examined the size of hake structures in sufficient detail to evaluate this possibility.

As in the Strait of Georgia, hake are the principal prey in the diet of harbour seals off southwestern Vancouver Island during April-July (Figure 26). The hake stock off southwestern Vancouver Island, in contrast to that in the Strait of Georgia, is largely migratory. The west coast stock spawns off California and Baja California in winter, but post-spawning fish migrate and school as far north as southern Vancouver Island (Bailey *et al*. 1982). Appreciable quantities of hake occur off southern Vancouver Island between mid-June and October (Beamish and McFarlane 1985). Thus, as in the Strait of Georgia, seals off southwestern Vancouver Island prey mainly on post-spawning hake that are seasonally available.

Since only small scattered concentrations of hake occur north of central Vancouver Island (G.A. McFarlane, pers. comm.), this prey is unlikely to be nearly as important as off southern Vancouver Island. Indeed, hake were absent from the few samples collected in Johnstone Strait and Masset Inlet during summer months, at which time they predominated the diet off southern Vancouver Island.

Pacific herring: The total annual consumption of herring in the Strait of Georgia study area was estimated at 3,206 tonnes (range 1,955-5,410 tonnes).

Although there appear to be small resident herring stocks in the Strait of Georgia, and many juvenile herring tend to remain within the Strait

throughout the year, the herring population is largely migratory (Taylor 1964; Hay *et al*. 1987; Hay *et al*. 1989). In late fall-early winter, adults enter the Strait of Georgia in preparation for spawning, which takes place in March-April. After spawning, most herring aged 2+ years and probably some of those aged 0+ and 1+ leave the Strait of Georgia to spend the summer off the southwest coast of Vancouver Island.

Herring stock assessments, estimated and published annually (e.g. Haist *et al*. 1988), represent only the spawning biomass of mature fish. The magnitude of the non-spawning herring biomass (i.e. juveniles of ages 0+, 1+ and 2+) is unknown and probably varies annually. A very crude estimate, however, is that it may be about one-third of total biomass (D. Hay, Nanaimo, B.C., pers. comm.). Due to the inherent variability in recruitment, estimates of spawning biomass are highly variable. Recent (1977/78-1986/87) estimates for the Strait of Georgia stock have ranged from 36,000-113,000 tonnes ($\bar{x}$=66,230 tonnes)(Haist *et al*. 1988). Commercial herring catches, taken mainly for roe, have ranged from 588 to 24,000 tonnes ($\bar{x}$=11,990 tonnes) over the same period (Haist *et al*. 1988). The annual consumption by harbour seals therefore represents about 4.8% (range 3.0-8.2%) of the mean recent spawning biomass, or perhaps 3.2% (range 2.0-5.5%) of total biomass, and 27% (range 16-45%) of the recent mean commercial harvest.

Seasonal patterns in herring predation also appear to reflect the availability of this prey species. In all non-estuary regions, predation on herring increased sharply during November-December (Figures 23-25), which coincided with the influx of pre-spawning herring from offshore waters. Interestingly, the increase was slightly later and less pronounced in the northern Strait, perhaps because most migratory herring arrived from the south through the Strait of Juan due Fuca and tended to school in the southern portions of the Strait of Georgia prior to spawning (R.W. Armstrong, Nanaimo, B.C, pers. comm). Once spawning was completed in March-April, herring immediately became less prevalent (Figures 23-24). However, the Southern Gulf deviated from this general pattern in that herring continued to be fairly important until May and June (Figure 25). As noted earlier (Section 5.3), these were predominately, though not exclusively, juveniles which are widely distributed in shallow water throughout the year (Hourston 1956). Further, seals in the Southern Gulf and elsewhere may have been preying upon small non-migratory stocks, which are scattered throughout the Strait (Hay 1986).

The same basic seasonal patterns were also evident in some estuaries, such as Comox Harbour, Mud-Fanny-Deep Bays and the Nanaimo River estuary (Figures 13-15). However, in others, such as the Shoal Islets, Cowichan Bay, Mill Bay and Port Moody, (Figures 16-19), herring were consumed uniformly or sporadically throughout the year. A cursory examination of the size of herring elements recovered from the latter estuaries suggests that most of the herring were juveniles, which are widely distributed in shallow areas throughout the year (Hourston 1956).

The limited data collected from other regions suggest that herring may be an important prey throughout much of British Columbia. For example, herring were the most predominant prey in Masset Inlet in June, off northwest Vancouver Island in February, and at the mouth of Johnstone Strait in July and September (Figure 26). However, the seasonality of predation on herring probably

varies depending on the migration patterns of local herring stocks. For instance, the prevalence of herring in the diet in Masset Inlet increased noticeably between April and June, which may reflect the greater availability of herring during spawning, which occurs 2-3 months later in Masset Inlet than in the Strait of Georgia (D. Hay, pers. comm.). The importance of herring in the diet in Johnstone Strait in July and October, in which months herring were a minor dietary component in the Strait of Georgia, may represent predation on local resident stocks (Hay 1986).

Salmonids: Total annual salmonid consumption in the Strait of Georgia was estimated at 398 tonnes (range 125-848 tonnes). Although seals inhabiting estuaries constituted only 5-17% ($\bar{x}$=10.3%) of the total population, they accounted for 30% of the total consumption of salmonids.

Except for small quantities of trout taken in estuaries, most of the salmonids consumed were Pacific salmon. No trout were identified in samples collected outside of estuaries. Total annual trout consumption was estimated at 4,345 kg, which represented only 1.1% of the total salmonid consumption. Trout predation was concentrated at 3 sites, which combined accounted for 89% of total consumption: Comox Harbour (2,005 kg), Port Moody (898 kg) and Boundary Bay-Fraser River (961 kg). Before interpreting these estimates any further, we should point out that: 1) our estimates of trout consumption are generally conservative as trout could not always be distinguished from Pacific salmon; 2) trout consumption may have, however, been exaggerated in two areas (Comox Harbour and Port Moody) because some of the salmonids were only tentatively identified as trouts; and 3) since trout comprised a minuscule portion of the overall diet (0.04%), the estimates are subject to large relative errors.

In Comox Harbour, about two-thirds of the trout consumed were taken during May-July, and 80% of these were smolt-sized fish that were tentatively identified as steelhead (see Section 4.1). The steelhead smolts were prevalent in three collections made during 20 May-20 July, 1988, which coincided with 24 April-2 June, 1988, hatchery releases of about 3,685 kg of steelhead (82,500 - 44.6 gm smolts)(H. Genoe, SEP, Comox, B.C., pers. comm.). Assuming the smolts were in fact steelhead, approximately 30% of the hatchery release was consumed by seals. However, the smolts could not be definitively discriminated from salmon, and much larger hatchery salmon releases preceded the May-July scat collections: 4.76 million 5.0-gm chinook (23,700 kg), 3.2 million 0.6-gm chum (1,840 kg) and 3.3 million 0.2-gm pink salmon (657 kg). The apparent preference for trout over salmon smolts may be attributable to their larger size at release (44.6 versus 0.2-8.0 gms). The remaining 1,075 kg of trout consumed in Comox Harbour were comprised of adult-sized fish taken primarily during July-October. These were tentatively identified as steelhead, but may also have been cutthroat. Based on the combined steelhead and cutthroat escapement (see Appendix III), seal predation on adults was estimated to be equivalent to 32% of the total escapement.

The 898 kg of trout consumed by seals in Port Moody could not be identified, but were taken in October-November when cutthroat, the only species

common in the area, were returning to rivers from the estuary (Appendix III). Based on the approximate mean cutthroat weight of 0.4 kg, we estimate that about 2,245 fish were consumed, but no escapement data were available for cutthroat trout in this area for comparison.

An estimated 961 kg of trout, tentatively identified as steelhead, were consumed by seals at the mouth of the Fraser River during October-November. The high consumption was not due so much to the fact that steelhead were an important dietary item ($\bar{x}$=2.7%), but rather to the large number of seals that congregated in this area during these months (Figure 10). Steelhead consumption in the Fraser River accounted for <1% of mean recent steelhead escapement (Appendix III). Only minute (<100 kg) quantities of trout were consumed in the remaining estuaries, and seal predation represented a small proportion (<3%) of escapement, except in the Shoal Islets estuary where the estimated 94 kg of trout consumed represented 9.9% of the mean recent escapement (Appendix III).

Harbour seal predation on Pacific salmon was confined almost exclusively to adult-sized fish. Outside of estuaries, salmon predation was lowest during February-May, increased during June-July, and peaked during August-December (Figures 22-25). Within estuaries, the timing was similar, but autumn peaks were generally better defined (Figures 12-20) and coincided with an influx of seals (Figures 10 and 11). These temporal patterns broadly coincided with the return of salmon to inshore waters and ultimately their natal rivers to spawn (see Appendix III). Thus, the harbour seal can be viewed as a terminal predator on salmon with predation becoming more intense as salmon concentrate en route to spawning, especially at the mouths of rivers in estuaries.

The consumption of salmon by harbour seals can only be compared to total escapement in very general terms for several reasons. First, escapement is generally highly variable, cyclic for some species, and poorly known for many of the smaller streams and creeks. Data on the timing, species composition, numerical abundance, weight of salmon escapement in the Strait of Georgia in recent years (1978-87) used in our comparison are summarized in Appendix III. Second, the species of salmon consumed could rarely be determined from remains recovered in scats (Section 4.2), such that it was impossible to directly partition total consumption among species.

Overall, the estimated 394 tonnes of salmon consumed by seals represented 2.8% of the mean escapement for the entire Strait of Georgia (Appendix III). However, salmon predation was concentrated in specific estuaries (Figures 12-20; Table 4), so predation rates differed among local stocks. In calculating predation rates for local stocks, we assumed that the 117.4 tonnes consumed within estuaries were salmon that would have spawned in adjacent rivers (see Appendix III). The 280.3 tonnes consumed outside of estuaries could not be directly associated with any local stock and were probably a mixture of many stocks en route to their natal rivers. If we assume that all stocks were randomly mixed prior to entering estuaries, the predation rate outside estuaries would have been uniformly 2.0% for all stocks in the Strait of Georgia. Adding this 2.0% to the predation rates calculated for within each estuary, we estimated the predation rate for individual estuaries (Table 6).

Predation rates, expressed as a percentage of escapement, typically varied from 2.6-10.7% but were much higher in two estuaries. Although salmon comprised only a minor portion of the diet in Mill Bay (Figure 18), the predation rate was over 300% of escapement because the latter was so low (Appendix III). This implied that seals in Mill Bay had either consumed more than three-quarters of salmon that returned to nearby Shawnigan Creek or, alternatively, seals may have ventured outside the estuary to prey on other stocks (or other salmon stocks had ventured into the estuary). The alternate explanation seems reasonable in that much larger salmon stocks pass Mill Bay en route to Goldstream River at the head of Saanich Inlet. The other atypically high predation rate (79.4%) was in Port Moody. Seals in this estuary must either have consumed almost half of the returning salmon or ventured outside the estuary to feed, although the latter would have entailed travelling quite some distance.

It was improbable that significant quantities of salmon had been consumed in estuaries other than those sampled, as they were only occasionally inhabited by few seals. Moreover, the sampled watersheds accounted for 82.9% of the total escapement biomass of salmon in the entire Strait of Georgia (see Appendix III).

As noted previously, the species composition of the Pacific salmon consumed by seals could not be directly established from scat contents. Alternatively, preliminary estimates of species composition were derived indirectly by assuming that seals were non-selective with respect to size or species of salmon consumed. In other words, the salmon consumption in each estuary was partitioned by species according to the relative numerical abundance of salmon species returning to each, and the consumption outside estuaries according to the overall relative numerical abundance of species in the entire Strait of Georgia. In very broad terms, the assumption of non-selectivity was probably realistic. Data from the Skeena River test fishery indicated that species of salmon in gillnets were preyed upon in roughly the same proportions they were caught (Olesiuk, unpubl. data), which suggested that seals were non-selective when all species were equally available. Moreover, predation on salmon was concentrated in the areas and months salmon were most abundant and presumably readily available. Finally, the timing of spawning broadly overlapped for most species of salmon, and the seasonal increases in both the prevalence of salmon in diets and the abundance of seals within estuaries coincided with these peaks. Nevertheless, seals likely exhibited some selectivity depending on the differences in behaviour, migration patterns, etc. among salmon species. Until additional studies (currently underway) have established selectivity coefficients, our estimates of consumption by species should be regarded as provisional.

The provisional estimates of the species composition of salmon consumed are given in Table 7. Predation rates differed slightly among species (2.89% for sockeye; 3.35% for coho; 3.02% for pink; 3.12% for chum; and 2.97% for chinook) due to the combined effect of among-estuary differences in the species composition of escapement and predation rates. Predation rates within estuaries, wherein the differences arose, were 0.93% for sockeye, 1.01% for pink, 1.04% for chinook, 1.63% for chum and 2.17% for coho. These indicated that predation rates tended to be lower (i.e. fewer seals congregated relative to the size of salmon runs) in estuaries supporting large sockeye and pink runs (i.e. Fraser River), and highest in estuaries with large chum and coho runs. Numeri-

cally, sockeye was the most important species (43.0%) followed by chum (27.8%), pink (21.1%), coho (4.9%), and chinook (2.4%). In terms of biomass, chum were the most important (39.5%), followed by sockeye (35.8%), pink (15.0%), chinook (4.9%) and coho (4.7%).

The few samples collected from outside the Strait of Georgia indicated that salmonid predation varied with region and season (Figure 26). Interestingly, salmonids comprised a very significant portion of the diet (30.1-30.2%) at the entrance to Johnstone Strait in July and September. This was much higher than in any non-estuary region in the Strait of Georgia, and was more comparable to the prevalence of salmon within estuaries at the height of spawning. The entrance to Johnstone Strait represents a constriction in the migration route of salmon and, as in estuaries, salmon may be especially concentrated and vulnerable to predation. For example, killer whales (*Orcinus orca*) congregate in this area during July-August and feed mainly on salmon (Bigg and Ellis, unpubl. data).

Plainfin midshipman: Overall, plainfin midshipman was the fourth most important prey species overall, ranking fifth both within and outside estuaries. Total annual consumption was estimated at 335.4 tonnes (range 74.5-773.7 tonnes), of which 33.5 tonnes was consumed in estuaries and 301.9 tonnes outside estuaries (Table 4).

Plainfin midshipman are neither commercially nor recreationally utilized in British Columbia. No estimates of stock size are available, but the species is considered common in the Strait of Georgia (Hart 1973). Predation was uniformly distributed (range 1.4-3.8%) among all estuaries but, outside of estuaries, was was concentrated in the Gulf Islands (Table 5). Both within and outside of estuaries, predation peaked during April-June (Figures 12 & 22). However, outside of estuaries (Figure 22), and within several estuaries such as the Nanaimo River estuary, Cowichan Bay and Mill Bay, there was a secondary peak during November-December. The earlier peak coincided with the spawning season during which males actively defend nests in shallow or intertidal waters (Arora 1948). The reasons for the later peak were unclear, as this species is thought to inhabit greater depths outside of the spawning season (Hay *et al.* 1989).

Lingcod: Total annual hexagrammid consumption was estimated at 310.8 tonnes (range 128.6-539.5 tonnes) of which 2.7 tonnes was consumed within estuaries and 308.1 tonnes outside of estuaries. The hexagrammids consumed were mainly lingcod (94.5% overall; 67.3% in estuaries and 96.0% outside of estuaries). Thus, total lingcod consumption was estimated at 293.7 tonnes and greenling consumption at 17.1 tonnes. The following discussion is therefore directed toward lingcod.

Although lingcod are commercially and recreationally important in the Strait of Georgia, no reliable estimates of the stock size in this area are available. However, decreases in commercial catches and catch-per-unit-effort suggest that stocks have been declining in recent years (Richards and Hand 1990).

The commercial catch in the Strait of Georgia declined steadily from historic highs of about 3,000 tonnes in the 1930-40s, to 1,200-1,600 tonnes in the 1950s, to a low of 96 tonnes in 1988. Creel surveys indicated that annual sport catches were generally on the order of 100-150 tonnes during 1980-88 ($\bar{x}$=131.6 tonnes) and declined only marginally during this period (Richards and Hand 1990). The annual consumption by harbour seals is thus roughly equivalent to the recent commercial and sport catches combined.

Predation on lingcod was confined almost exclusively to November-April, the period males were defending nests (Low and Beamish 1978) and were probably most susceptible to predation. Although evident in both the Gulf Islands and Northern Gulf, the seasonal peak in lingcod predation was much more pronounced in the latter (Figures 23 & 24). Within each region, lingcod predation was highly variable among sites. For example, lingcod was especially prevalent in several large scat collections obtained from Gowland Harbour on the southeast coast of Quadra Island - present in 17 of 35 (48.6%) and 18 of 32 (56.3%) of the samples collected from this site in January and March respectively. Although lingcod were also prevalent at several other sites sampled during this period (e.g. 4 of 6 [66.7%] samples collected at Douglas Island off Nanoose Bay in December and 4 of 15 [26.8%] collected from Danger Reef in Trincomali Channel in April), lingcod were scarce or absent in most collections. Because lingcod predation was highly localized, our estimates of annual consumption were subject to considerable sampling bias. Specifically, the importance of this prey in the Northern Gulf (Table 4) may have been inflated due to the disproportionately large number of samples collected from Gowland Harbour. The magnitude of lingcod predation within the Southern Gulf could not be reliably established as few scats were collected from this region during November-April.

The few samples collected from outside the Strait of Georgia indicated that lingcod may be a more important prey, and predation not as confined to spawning fish. As herring probably became less available when they migrated offshore after spawning, the importance of lingcod increased off southeast Vancouver Island during April-July (Figure 26). Lingcod were also a predominant prey in the few samples collected off northwest Vancouver Island in February (Figure 26).

7. DISCUSSION

Our study has illustrated some of the limitations as well as the advantages of scat analyses. We conclude that, at present, scat analysis alone cannot be used to determine the absolute quantities of prey consumed (i.e. feeding rates), nor are we optimistic advances in scat methodology will enable such estimates. Our results, as those of many others (Prime 1979; Hawes 1983; McConnell *et al*. 1984; da Silva and Neilson 1985; Murie and Lavigne 1985; Jobling and Breiby 1986; Jobling 1987; Dellinger and Trillmich 1988; Harvey 1989), indicate that the prey remnants recovered from scats represent only a portion of those actually consumed, the remainder having been completely digested or diges-

ted beyond recognition. The proportion recovered appears to vary with a host of factors, including the size and species of prey, the particular structures used to identify prey and their robustness, and between individual seals. Derivation of correction coefficients to account for all of these factors would seem to be an insurmountable task. To be of predictive value, these coefficients would have to vary less among prey species than between individual seals. Evidence compiled to date suggests this may not be the case. For example, Dellinger and Trillmich (1988) reported that sprat and herring otoliths recovery rates ranged from 1.3-87.3% for sea lions and 3.8-80.0% for fur seals, yet they found no significant differences among these prey species for either predator. Similarly, Harvey (1989) reported that shiner perch otolith recovery rates for a pair of harbour seals varied between 28.6% and 100%, which was comparable to the range in the mean otolith recovery rates (24.5-89.4%) for the 10 different prey species he examined.

Even if such coefficients could be derived, one would have to establish the period over which the prey in the scats had been consumed to estimate feeding rates. It is unlikely that pinnipeds defecate on a regular schedule. Bigg and Fawcett (1985) observed that subsequent feeding stimulated the defecation of an earlier meal in northern fur seals whereas Dellinger and Trillmich (1988) noted that movement and wetting appeared to enhance defecation. Finally, our experience in collecting harbour seal scats, as well as California and Steller sea lion scats, indicates that it is not usually possible to collect whole scats, or to ascertain what fraction of the scat may have been washed away by tides or rain prior to collection. For these reasons, we suggest that to estimate prey consumption, it will continue to be necessary to synthesize information on the diet composition obtained from scat analysis with independent estimates of feeding rates (e.g. based on stomach contents or derived from captive feeding studies).

Although it may not be possible to estimate the absolute quantity of prey consumed from scats, we believe that further refinements in methodology will enable improved estimates of the relative volumes of prey consumed in meals. Harvey's (1989) predictive regression between the recovery rate and robustness of otoliths represents a major step toward this end. However, since otoliths alone provide an incomplete and biased representation of diet, these analyses must be broadened to include other structures. Our volumetric weighting coefficients for hake and herring, based on the relative recovery rates of various structures, represent a first attempt. However, these indices must now be established for other predator and prey species and their validity assessed in captive studies.

We contend that scat analysis has evolved to the extent that it provides reliable information on the relative frequency of prey, at least of fishes, in pinniped diets. However, we have demonstrated that an unbiased representation of diet can only be achieved by utilizing a wide variety of skeletal structures, not just otoliths, to identify prey. In support, Gearin *et al.* (1988) recently re-examined sea lions scats using various structures and noted that in previous analyses based on otoliths "we would have grossly underestimated the frequency of occurrence of salmonids and also dogfish shark". The revised diet was comprised of 22.6% dogfish, which had not previously been identified as prey, and 17.6% salmon, though only 4 salmon otoliths were recovered. Indeed, much of the

criticism levied toward scat analyses (da Silva and Neilson 1985; Jobling and Breiby 1986; Jobling 1987) can largely be attributed to the preoccupation with otoliths, and not to the general utility of scat analyses.

In many circumstances, particularly when meals are comprised of only one or a few species, the relative frequency of prey in the diet will provide a good indication of their relative importance. For example, our analysis of the northern fur seal data base showed that results similar to those obtained by volumetric analysis can be attained using the split-sample frequency index without knowledge of the prey-volumes. Moreover, based on the frequency of prey in scats, coupled with a series of realistic assumptions, we were able to calculate meaningful upper and lower limits of the contribution of prey in the diet of harbour seals, and hence recognize the predominant and important prey species.

Since scat collections are benign and provide accurate information on diet composition, they represent a powerful tool for examining seasonal and regional variability in diet. The present study, as well as our experience with California and Steller sea lions and northern fur seals, suggests that such variation is a major potential source of bias in estimating prey consumption. Although far more harbour seal scats were examined in the present study than have been available in previous studies, and our study focused on a relatively localized area, we feel that our sample sizes were barely adequate to appreciate the basic dynamics of harbour seals predation, and were insufficient to quantify some of the more subtle aspects (e.g. trout and lingcod predation). Moreover, the limited data collected from other regions suggested that feeding patterns were highly localized depending on the local availability of prey, such that extrapolations between areas must be made with extreme caution. It is difficult to imagine how such comprehensive diet assessments could be undertaken using any other method. For example, assuming that 50% of the seals killed would be lost (Bigg 1969) and 50% of stomachs recovered would be empty (Spalding 1964; Boulva and McLaren 1979), it would have been necessary to kill 11,300 seals, or 79% of the total Strait of Georgia population, to obtain an equivalent number of stomachs that contained prey.

Our finding suggest, as those of others (Scheffer and Slipp 1944; Spalding 1964; Rae 1973; Boulva and McLaren 1979; Pitcher 1980; Beach *et al.* 1982; Brown and Mate 1983; Harkonen 1987; Payne and Selzer 1989), that the harbour seal is an opportunistic predator that is capable of adjusting its feeding habits to take advantage of locally and seasonally abundant prey. Indeed, few generalizations concerning their prey preferences are possible. While some investigators have noted a preference for small-schooling fishes (Boulva and McLaren 1979; Pitcher 1980; Payne and Selzer 1989) others have noted a preference for benthic or epi-benthic species (Brown and Mate 1983). Our study suggested that seals generally foraged near-shore throughout the water column, but occasionally preyed on benthic species such as lingcod, flatfishes and sandlance when pelagic species were less available.

Preliminary analysis of 1,861 scats from Steller and California sea lions wintering off southern Vancouver Island (Olesiuk and Bigg 1988; Olesiuk unpubl. data) indicated that their feeding habits were in many respects similar to those of harbour seals. Upon their arrival off southern Vancouver Island in

September-November, sea lions fed primarily on hake and to a lesser degree salmon, as did harbour seals during the same period. Both predators, however, switched to herring when this prey moved inshore to spawn during December-March. Nevertheless, harbour seals and sea lions differed in two obvious respects. Spiny dogfish comprised an important dietary item (ranked 3rd) for the latter but were never found in harbour seal scats. The absence of this prey, even though it was abundant in some of the estuaries inhabited by harbour seals (G. Ellis, unpubl. data), may indicate a general preference toward smaller prey. Second, sea lions tended to follow their prey and formed large herds where prey were concentrated. Although local movements of harbour seals related to prey availability were also evident (e.g. migration into estuaries during salmon spawning) they were not nearly as pronounced as those of sea lions. For example, a very large pre-spawning concentration of herring (approximately 20,000 tonnes; R.W. Armstrong, pers. comm.) in Northumberland Channel, near Nanaimo, attracted over 1,700 sea lions, but less than 100 harbour seals.

In the Strait of Georgia, hake and herring were by far the two most predominant prey and combined accounted for 75% of the overall diet. One would therefore expect hake and herring stocks to play an important role in regulating the size of the harbour seal population, if in fact carrying capacity is food-limited. The current (1988) population, which is thought to be near or perhaps slightly above historic levels (Olesiuk and Bigg, in prep.), consumed an estimated 3.2% of the total hake biomass and 3.5% of the total herring biomass annually. However, only portions of the total stock may have been accessible to seals, the remainder being too deep, far offshore, or concentrated. Interestingly, both of these prey appeared to be only seasonally available in the Strait of Georgia, but in an inverse manner to one another. Hence, perhaps fortuitously, these two prey provided an abundant year-round source of food. It may be this arrangement that accounts for the much higher density of seals in the Strait of Georgia compared to other regions of British Columbia (Olesiuk *et al.* in press).

Although hake and herring represented the major food items, many other prey were taken on an opportunistic basis. Predation on these prey appeared to be largely limited to the specific periods each was most vulnerable. For example, salmon were consumed mainly as they concentrated en route to their natal rivers to spawn, lingcod and plainfin midshipman during their spawning season as males were defending nests, and trout as they were released in large quantities from hatcheries or returning to rivers from estuaries. Since each of these prey comprised a relatively minor component of the overall diet, they probably play little role in regulating seal abundance. Thus, seals preying on these species need not be as prudent as Slobodkin (1961) generally hypothesized. Rather, the situation may be analogous to a mixed-species fishery, in which abundant stocks can support high fishing effort and rates, and ultimately lead to the over-utilization and demise of the rarer stocks. For instance, although lingcod stocks in the Strait of Georgia may have been depleted to the extent that they might no longer be commercially viable (Richards and Hand 1990), this species continues to be vulnerable and preyed upon during spawning. Similarly, the large concentrations of seals attracted to estuaries, presumably by other prey or by haulout conditions, may exact a heavy toll on vulnerable resident fish such as trout and on smaller salmon stocks. It is these situations that may be of greatest concern in holistic fisheries management.

By their nature, these localized conflicts are restricted to the areas and times that certain prey are especially vulnerable. Scat analysis is perhaps the best-suited approach for obtaining a broad overview of the diet, and hence for identifying these conflicts. Once identified, the conflicts can be investigated in greater detail using more-directed and higher-resolution techniques, such as direct observations (e.g. Gearin *et al.* 1988; Brown and Mate 1983; Ellis, unpubl. data).

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Table 1. Fish prey species identified in harbour seal scats and number of occurrences of each. Taxonomy follows Hart (1973).

Code:	Class: Family: Species:	Common name:	Number of Occurrences:
FIS	Osteichthyes	Bony fishes	5,081
GAD	Gadidae	Cods	1,785
HAK	*Merluccius productus*	Pacific hake	1,531
POL	*Theragra chalcogramma*	Walleye pollock	43
TOM	*Microgadus proximus*	Tomcod	24
PCD	*Gadus macrocephalus*	Pacific cod	13
CLU	Cluepidae	Herrings and anchovies	1,694
HER	*Clupea harengus pallasi*	Pacific herring	1,685
ANC	*Engraulis mordax mordax*	Northern anchovy	7
SHA	*Alosa sapidissima*	American shad	2
SAL	Salmonidae	Salmon and trouts	451
TRT	*Salmo/Salvelinus* spp.	Trout	34
CHN	*Oncorhynchus tshawytscha*	Chinook salmon	5
CHM	*Oncorhynchus keta*	Chum salmon	1
CHO	*Oncorhynchus kisutch*	Coho salmon	1
MID	Batrachoididae	Toadfishes	234
MID	*Porichthys notatus*	Plainfin midshipman	234
SFP	Embiotocidae	Surfperches	221
SHP	*Cymatogaster aggregata*	Shiner perch	171
PPR	*Rhacochilus vacca*	Pile perch	21
SFX	spp.	Not surf or pile perch	2
SCP	Cottidae	Sculpins	159
SSC	*Leptocottus armatus*	Staghorn sculpins	68
OLG	*Oligocottus* spp.	Tidepool/Fluffy/Saddleback	19
BSC	*Enophrys bison*	Buffalo sculpin	3
BLC	*Malacocottus kincaidi*	Blackfin sculpin	1
GSC	*Myoxocephaus polyacanthocephalus*	Great sculpin	1
FLF	Pleuronectidae (+Bothidae?)	Flatfishes	150
SFL	*Platichthys stellatus*	Starry flounder	16
ESL	*Parophrys vetulus*	English sole	6
AFL	*Atheresthes stomias*	Arrowtooth flounder	1
REX	*Glyptocephalus zachirus*	Rex sole	1
RSL	*Lepidopsetta bilineata*	Rock sole	1
HEX	Hexagrammidae	Lings	83
LIN	*Ophiodon elongatus*	Lingcod	70
GRN	*Hexagrammus/Oxylebius* spp.	Greenlings	10
ROK	Scorpaenidae	Rockfishes	68
SAN	Ammodytidae	Sand lances	67
SAN	*Ammodytes hexapterus*	Pacific sand lance	67

Table 1. (cont'd)

Code:	Class: Family: Species:	Common name:	Number of Occurrences:
SML	Osmeridae	Smelts	46
EUL	*Thaleichthys pacificus*	Eulachon	29
RSM	*Osmerus mordax dentex*	Rainbow smelt	1
STK	Gasterosteidae	Sticklebacks	21
STK	*Gasterosteus aculeatus*	Three-spined stickleback	21
EEL	Zoarcidae	Eelpouts	9
BEP	*Lycodopsis pacifica*	Blackbelly eelpout	1
GUN	Pholidae	Gunnels	9[1]
PEN	*Apodichthys flavidus*	Penpoint gunnel	1
PRK	Steichaeidae	Pricklebacks	3[1]
RON	Bathymasteridae	Ronquills	1
WOL	Anarchichadidae	Wolffishes	1
WOL	*Anarrhichthys ocellatus*	Wolf-eel	1
CLN	Gobiesocidae	Clingfishes	1
OTH	Other unidentified fishes	(at least 8 species)	11
UND	Unidentifiable fishes	(could be any of the above)	67
CAR	Chondrichthyes	Cartilagenous fishes	21
SKA	Rajidae	Skates	21
AGN	Agnatha	Hagfishes and lampreys	7
LAM	Petromyzonidae	Lampreys	7

[1]Possibly some confusion between these two families.

Table 2. Summary of the mean number of elements and total and mean number of structures used to identify the more important prey species in scat samples. An element is defined as any identifiable prey remnant and a structure as particular type of element. For example, in a sample containing two herring otoliths and three herring vertebrae, herring would be represented by five elements and two structures.

Prey:	Mean number of elements:	Number of structures	
		Mean:	Total:
GAD	32.4	6.1	47
CLU	59.4	3.5	44
SAL	17.3	2.3	50
MID	18.5	3.4	31
SFP	57.5	3.0	32
FLF	31.4	3.5	39
SCP	40.5	3.5	39
HEX	10.2	2.4	26
ROK	4.8	2.5	34
SAN	29.9	1.9	17
SML	11.8	1.6	13
CEP	2.9	1.5	3
Mean[1]:	38.7	3.4	97[2]

[1]weighted mean for all prey species.
[2]total for all prey species combined.

Table 3. Legend showing pattern codes used to denote prey in Figures 12-20 and Figures 22-26.

* includes American Shad for SW Vancouver Island

Table 4. Estimated annual prey consumption (tonnes) by harbour seals in the Strait of Georgia study area during 1988. Note that because the estimates for each estuary and region were derived using a high-level stratification, and the estimates for all estuaries and non-estuary sites (i.e. Subtotals and Total) using a low-level stratification, the former do not exactly sum to the latter. Species codes are as per Table 1. Area codes are: CX Comox Harbour; MF Mud-Fanny-Deep Bays; NA the Nanaimo River estuary; SI Shoal Islets; CW Cowichan Bay; MB Mill Bay; SQ Squamish River; PM Port Moody; BF Boundary Bay-Fraser River; NG Northern Gulf; GI Gulf Islands; and SG Southern Gulf.

	Estuaries										Non-estuaries				Grand
Prey:	CX:	MF:	NA:	SI:	CW:	MB:	SQ:	PM:	BF:	Subtot:	NG:	GI:	SG:	Subtot:	Total:
GAD	40.3	22.2	17.9	46.3	10.7	28.4	4.8	19.3	116.8	453.8	2,141.2	1,215.9	409.7	4,013.1	4,466.9
HER	43.4	64.7	17.3	18.2	13.0	8.1	3.2	14.9	43.8	244.2	1,044.0	901.0	843.6	2,962.1	3,206.3
SAL	30.7	3.7	5.0	0.8	9.0	0.7	1.6	5.4	89.8	117.4	140.1	83.5	96.8	280.3	397.7
MID	5.8	4.9	0.9	1.7	0.6	1.1	0.3	1.7	7.7	33.5	42.4	124.5	0.7	301.9	335.4
HEX	0.4	0.1	0.1	0.3	0.1	0.2	0.0	0.2	0.4	2.7	393.0	29.9	30.3	308.1	310.8
SFP	4.4	8.2	0.3	0.7	2.5	0.7	0.4	2.8	92.0	39.1	107.7	55.4	8.0	190.5	229.6
CEP	1.3	2.1	1.5	1.3	1.6	0.5	0.4	1.2	6.6	19.2	79.4	67.2	30.3	189.0	208.2
FLF	7.8	11.8	0.1	0.3	0.8	0.1	0.3	1.0	39.7	31.2	41.6	24.0	29.1	91.6	122.8
SCP	9.6	3.5	0.1	0.1	1.0	0.8	0.3	1.6	46.5	35.5	15.7	17.1	57.9	78.5	113.9
ROK	0.3	6.1	0.0	0.2	0.6	1.3	0.2	0.2	1.1	7.3	111.3	15.7	22.2	104.5	111.8
OTH	6.1	7.1	0.3	0.6	1.2	1.0	0.3	3.9	12.3	28.0	22.5	40.0	371.0	180.8	208.8
UND	2.1	4.4	0.3	0.2	0.6	0.1	0.1	0.3	12.9	11.2	185.1	33.1	38.5	169.9	181.2
Total	152.2	138.8	43.8	70.7	41.7	43.0	11.9	52.5	469.6	1,023.1	4,324.0	2,607.3	1,938.1	8,870.9	9,893.4

Table 5. Potential range in the absolute importance of important prey in the Strait of Georgia. Lower and upper limits were calculated by assuming that prey comprised entire and negligible portions of mixed meals respectively (see Sections 5.1e and 6.2 for details). Numbers in parentheses indicate magnitude of difference between limits and point estimates (in relative terms for percent of diet and absolute terms for annual consumption). All estimates were derived using a low-level stratification. Prey codes are given in Table 1.

	Percent of Diet			Annual consumption (tonnes)				
Prey:	Estimate:	Lower limit:		Upper limit:	Estimate:	Lower limit:		Upper limit:	
GAD	45.1	28.0	(0.62)	60.9 (1.35)	4,466.9	2,773.3	(1693.6)	6,030.4	(1563.5)
HER	32.4	19.8	(0.61)	54.7 (1.69)	3,206.3	1,955.4	(1205.9)	5,409.5	(2203.2)
SAL	4.0	1.3	(0.33)	8.6 (2.15)	397.7	124.5	(273.2)	848.3	(450.6)
MID	3.4	0.8	(0.23)	7.8 (2.29)	335.4	74.5	(260.9)	773.7	(438.3)
HEX	3.1	1.3	(0.42)	5.4 (1.74)	310.8	128.6	(182.2)	539.5	(228.7)
SFP	2.3	0.5	(0.22)	5.4 (2.34)	229.6	52.1	(177.5)	537.4	(307.8)
CEP	2.1	0.0	(0.00)	5.9 (2.81)	208.2	1.4	(206.8)	588.6	(380.4)
FLF	1.2	0.5	(0.42)	2.9 (2.42)	122.8	49.2	(73.6)	285.8	(163.0)
SCP	1.2	0.1	(0.08)	3.1 (2.58)	113.9	8.7	(105.2)	310.1	(196.2)
ROK	1.1	0.4	(0.36)	2.4 (2.18)	111.8	44.3	(67.5)	239.6	(127.8)
UND	1.8	1.0	(0.56)	3.0 (1.67)	181.2	103.6	(77.6)	295.6	(114.4)
Mean:	-	-	(0.35)	- (2.11)	-	-	-	-	-

Table 6. Estimated salmon predation rates within individual estuaries expressed as a percentage of mean total escapement biomass. Estuary codes are given in Table 4.

Estuary:	Predation rates		
	Outside estuary:	Within estuary:	Total:
CX	2.0	7.8	9.8
MF	2.0	8.7	10.7
NA	2.0	2.1	4.1
SI	2.0	0.6	2.6
CW	2.0	1.6	3.6
MB	2.0	318.2	320.2
SQ	2.0	0.2	2.2
PM	2.0	79.4	81.4
BF	2.0	0.9	2.9

Table 7. Provisional estimates of species composition by number (and tonnes) of Pacific salmon consumed in the Strait of Georgia study area in 1988. Estimates are provisional as they are contingent upon the unverified assumption that seal predation was non-selective with respect to size and species of salmon. Note that the estimates for individual estuaries were derived using a high-level stratification whereas those for non-estuaries using a low-level stratification. As a result, the total consumption is slightly (7.4%) greater than that given in Table 5 (after trout consumption is subtracted from the latter).

Area:	Sockeye:	Coho:	Pink:	Chum:	Chinook:	Total:
Comox Harbour	3 (0.01)	1,364 (3.68)	980 (2.25)	4,836 (22.25)	76 (0.51)	7,259 (28.70)
Fanny-Deep-Mud Bays	0 (0.00)	94 (0.25)	46 (0.10)	672 (3.09)	0 (0.00)	812 (3.44)
Nanaimo River	0 (0.00)	65 (0.18)	0 (0.00)	988 (4.55)	32 (0.21)	1,085 (4.94)
Shoal Islets	0 (0.00)	7 (0.02)	0 (0.00)	146 (0.67)	3 (0.02)	155 (0.71)
Cowichan Bay	0 (0.00)	385 (1.04)	0 (0.00)	1,613 (7.42)	75 (0.50)	2,073 (8.96)
Mill Bay	0 (0.00)	244 (0.66)	0 (0.00)	0 (0.00)	0 (0.00)	244 (0.66)
Squamish River	0 (0.00)	25 (0.07)	7 (0.02)	315 (1.45)	5 (0.04)	354 (1.58)
Port Moody	0 (0.00)	818 (2.21)	0 (0.00)	500 (2.30)	0 (0.00)	1,318 (4.51)
Boundary B.-Fraser R.	16,949 (45.76)	537 (1.49)	8,151 (18.75)	3,800 (17.49)	806 (5.40)	30,243 (88.89)
Non-estuaries	39,098(105.57)	3,843 (10.38)	18,389 (42.29)	23,455(107.90)	2,115(14.17)	86,900(280.30)
Total:	56,050(151.34)	6,382 (19.98)	27,573 (63.41)	36,325(167.12)	3,112(20.85)	130,443(422.69)

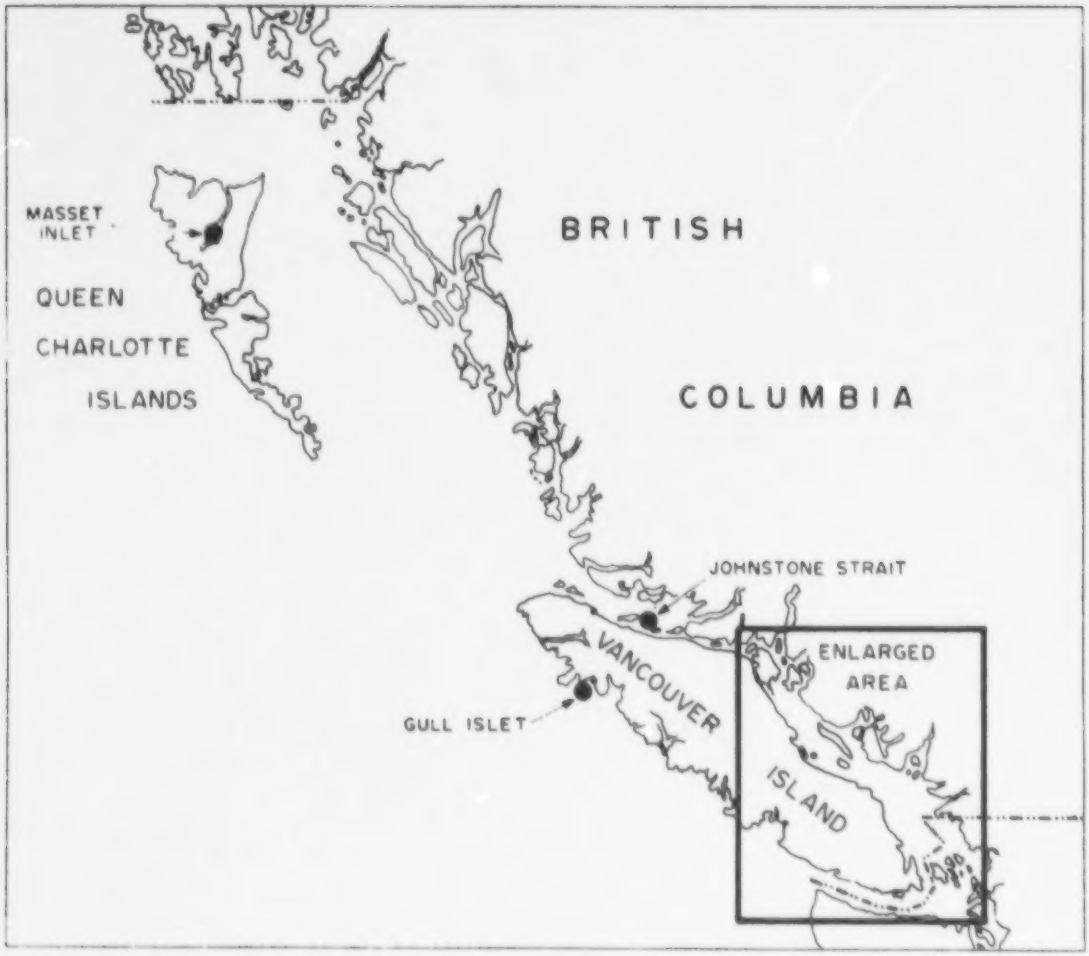
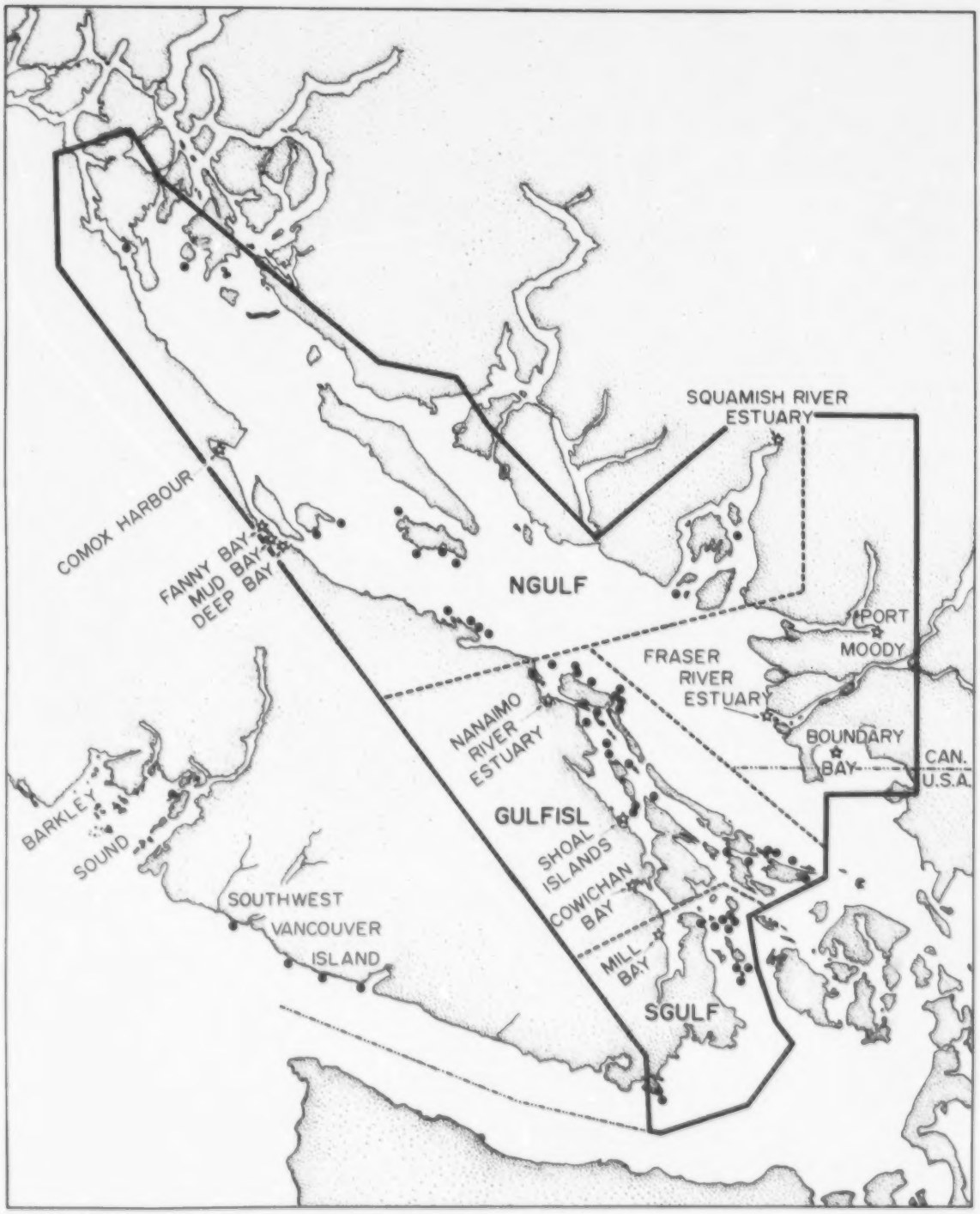


Figure 1. Overview map of British Columbia showing scat collection locations. Collection sites within the enlarged area are shown in Figure 2.

Figure 2. Strait of Georgia study area (solid line) showing boundaries of non-estuary regions (dashed lines), and location of all non-estuary (circles) and estuary (stars) scat collection sites.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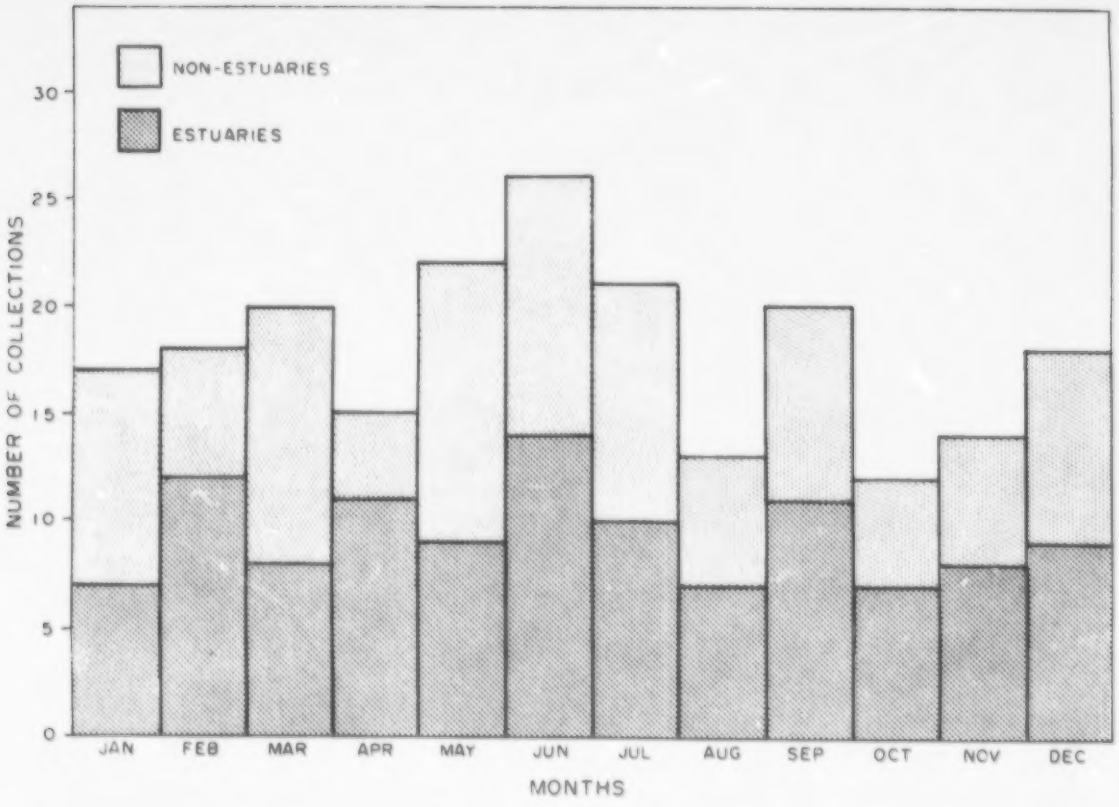
COMOX HARBOUR
FANNY BAY
MUD BAY
DEEP BAY
NGULF
PORT MOODY
FRASER RIVER ESTUARY
NANAIMO RIVER ESTUARY
BOUNDARY BAY
CAN.
U.S.A.
BARKLEY SOUND
GULFISL
SHOAL ISLANDS
COWICHAN BAY
SOUTHWEST VANCOUVER ISLAND
MILL BAY
SGULF

Figure 3. Numbers of scat a) collections and b) samples collected in the Strait of Georgia by month within estuaries and outside estuaries.


NON-ESTUARIES
ESTUARIES
NUMBER OF COLLECTIONS
0
5
10
15
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25
30
JAN
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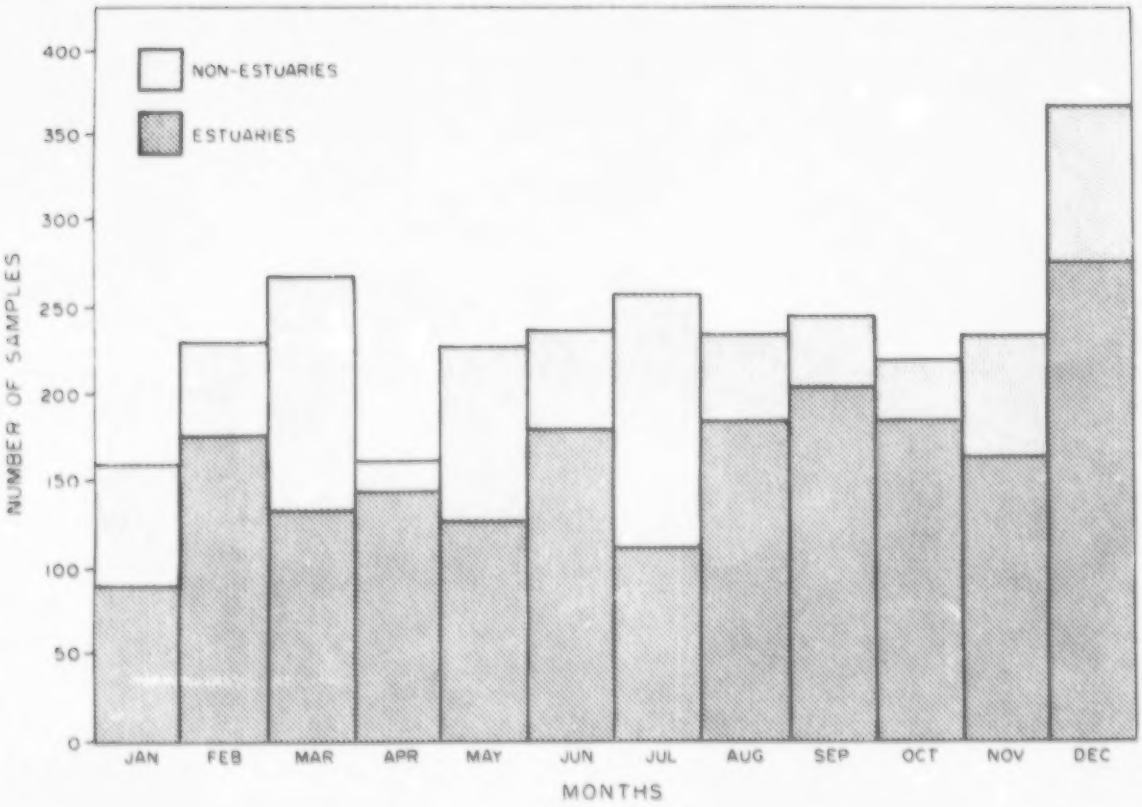
NON-ESTUARIES
ESTUARIES
NUMBER OF SAMPLES
0
50
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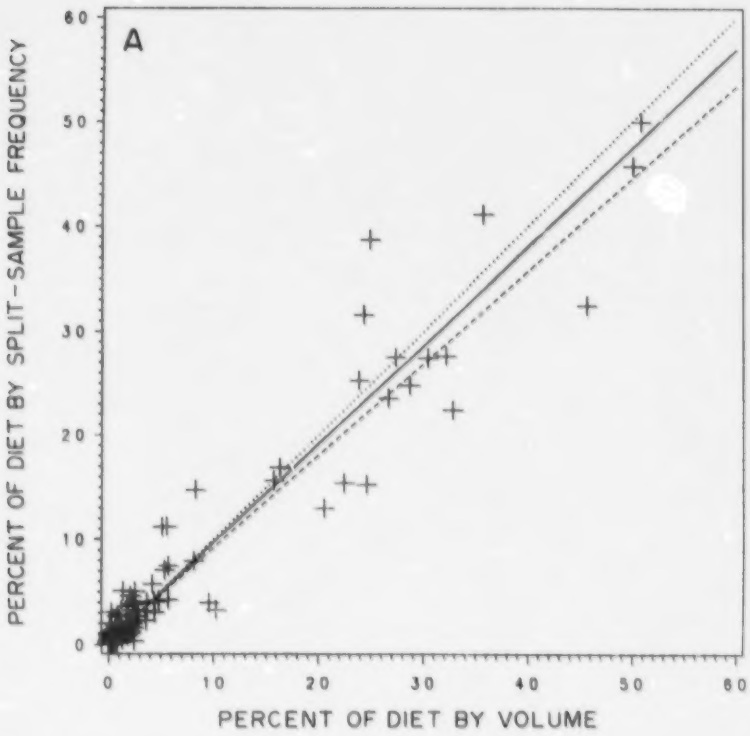
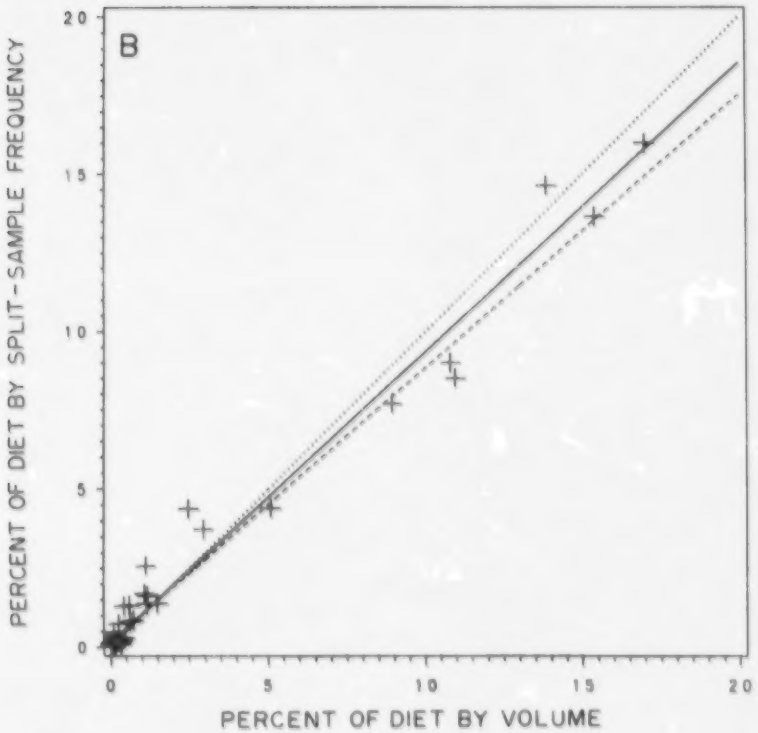
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
MONTHS

Figure 4. Comparison of the estimated relative importance of fish prey in the diet of northern fur seals by volumetric and by split-sample frequency of occurrence indices for: a) individual regions and b) all regions combined. The dotted lines denotes the 1:1 agreement lines and the solid lines the functional regressions fitted to the data. For comparison, the dashed lines show the functional regression between conventional frequency of occurrence and volumetric indices (data not plotted).


A
PERCENT OF DIET BY SPLIT-SAMPLE FREQUENCY
PERCENT OF DIET BY VOLUME
0
10
20
30
40
50
60


B
PERCENT OF DIET BY SPLIT-SAMPLE FREQUENCY
PERCENT OF DIET BY VOLUME
0
5
10
15
20

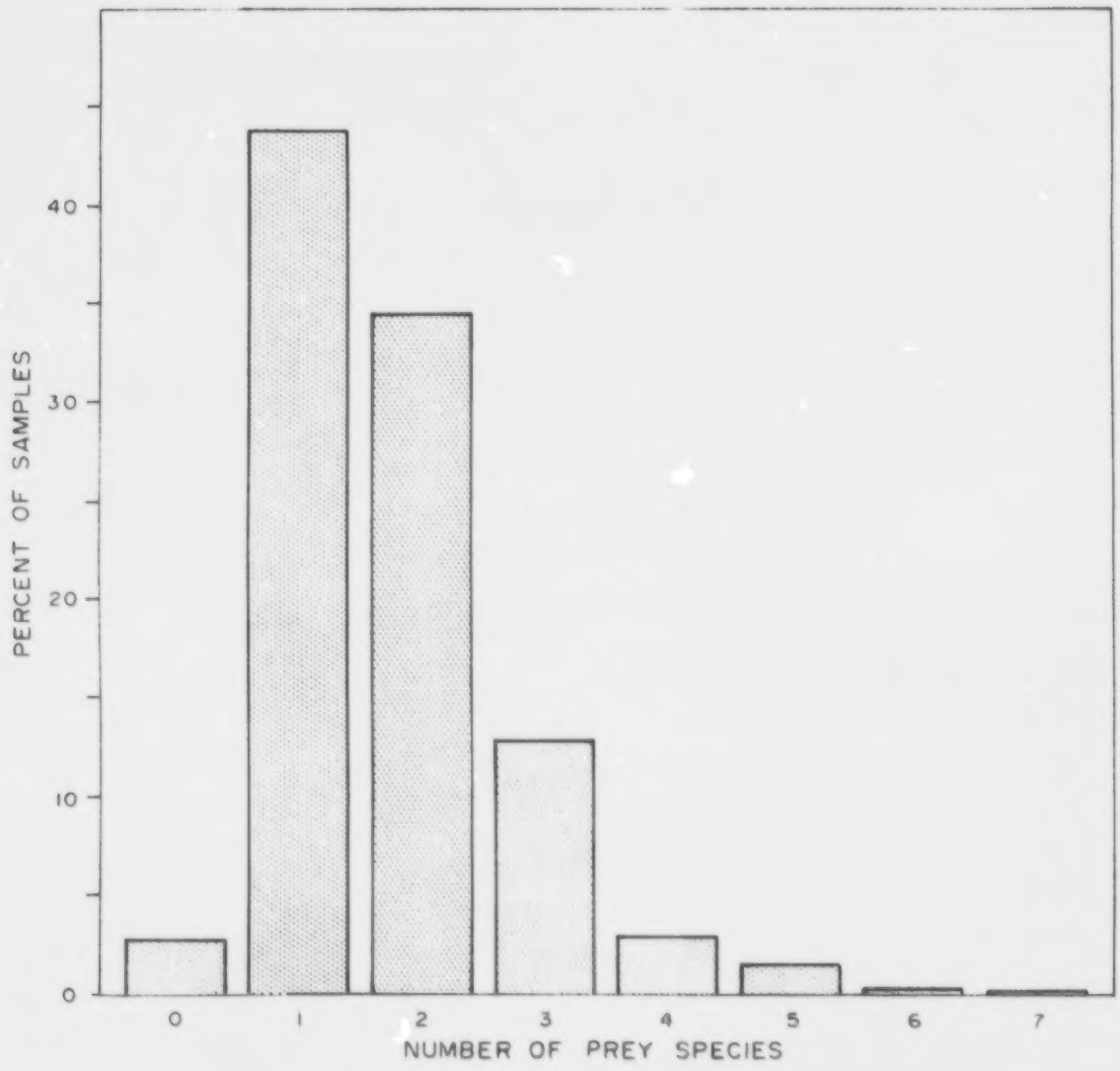


Figure 5. Frequency distribution of the number of different prey species identified per scat sample.

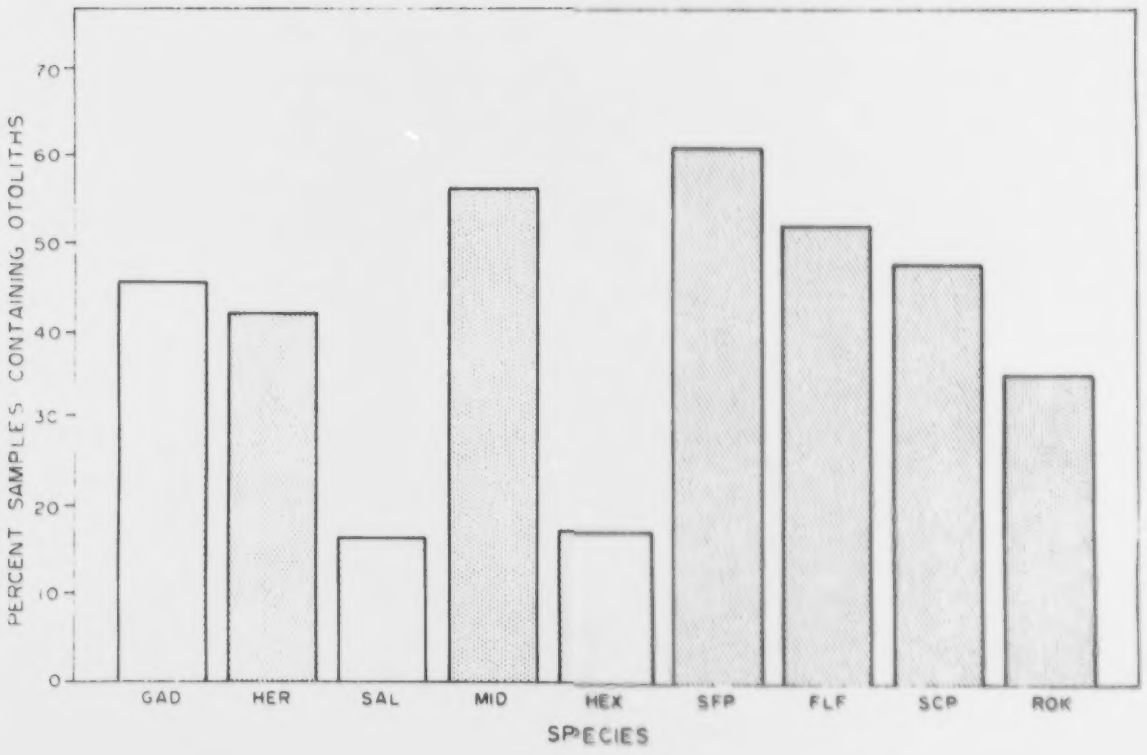


Figure 6. Proportion of scat samples in which prey were represented by their otoliths. Prey codes are defined in Table 1.

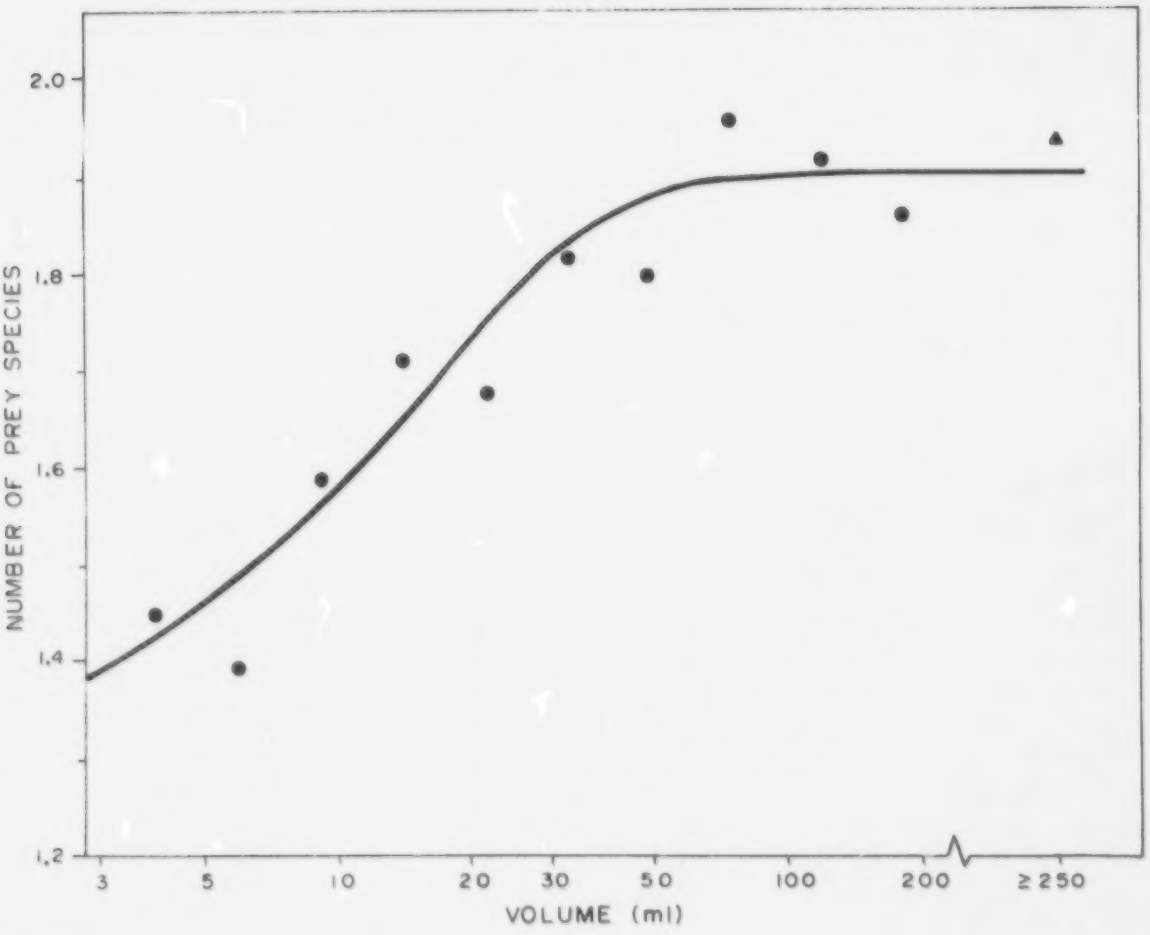
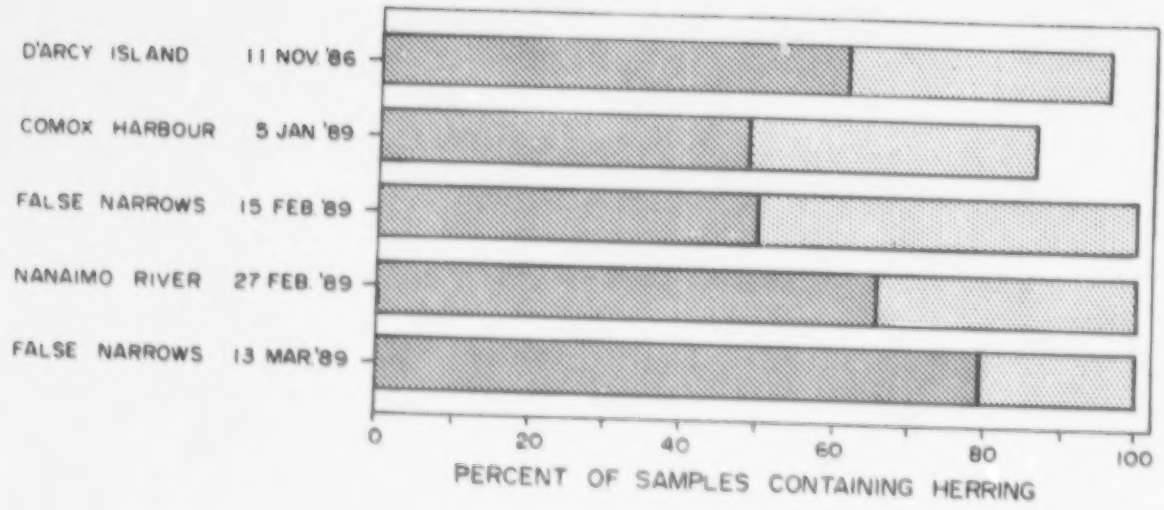
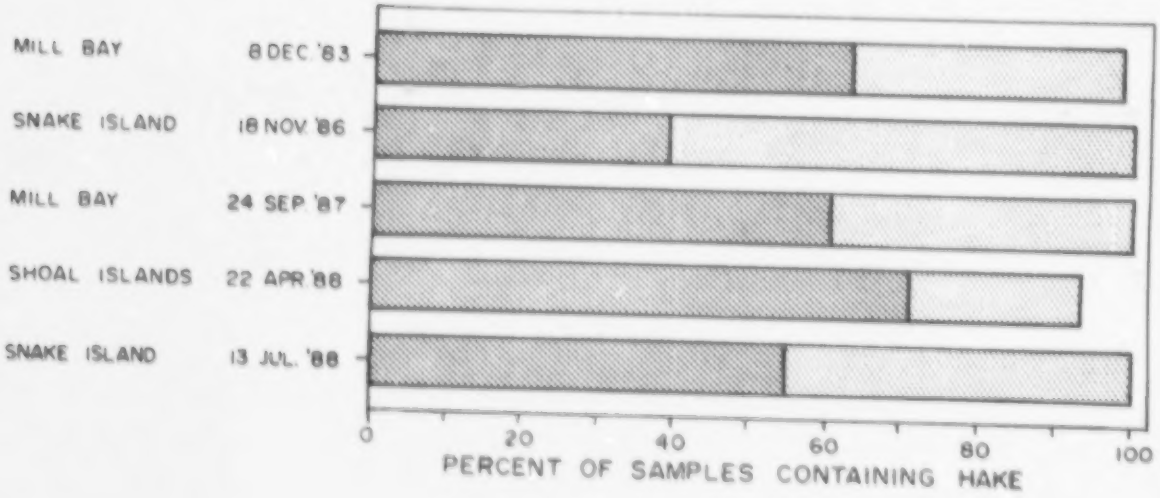
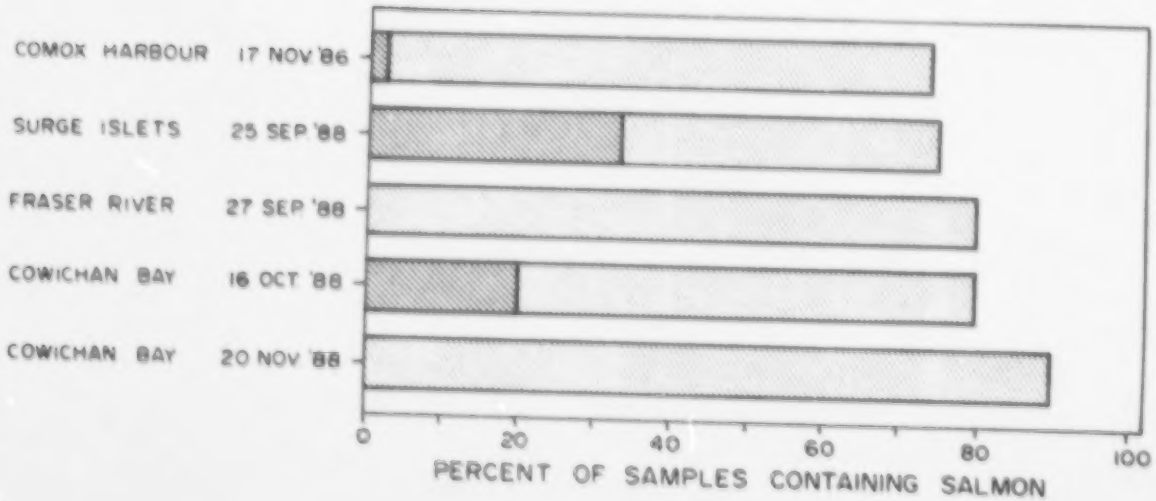


Figure 7. Mean number of prey species identified in scat samples as a function of sample-volume. Note that data were grouped into volume-categories on a logrithmic scale. The trend line denotes an asymptotic regression fitted to the ungrouped data.

Figure 8. Proportion of scat samples containing a) herring, b) hake, and c) salmonids for selected collections in which each was the focal prey. Shaded bars indicate the percent of samples in which the prey occurred and the dark portion of the bars the percent of samples in which prey were represented by their otoliths.


D'ARCY ISLAND 11 NOV '86
COMOX HARBOUR 5 JAN '89
FALSE NARROWS 15 FEB '89
NANAIMO RIVER 27 FEB '89
FALSE NARROWS 13 MAR '89
0
20
40
60
80
100
PERCENT OF SAMPLES CONTAINING HERRING


MILL BAY 8 DEC '83
SNAKE ISLAND 18 NOV '86
MILL BAY 24 SEP '87
SHOAL ISLANDS 22 APR '88
SNAKE ISLAND 13 JUL '88
0
20
40
60
80
100
PERCENT OF SAMPLES CONTAINING HAKE


COMOX HARBOUR 17 NOV '86
SURGE ISLETS 25 SEP '88
FRASER RIVER 27 SEP '88
COWICHAN BAY 16 OCT '88
COWICHAN BAY 20 NOV '88
0
20
40
60
80
100
PERCENT OF SAMPLES CONTAINING SALMON

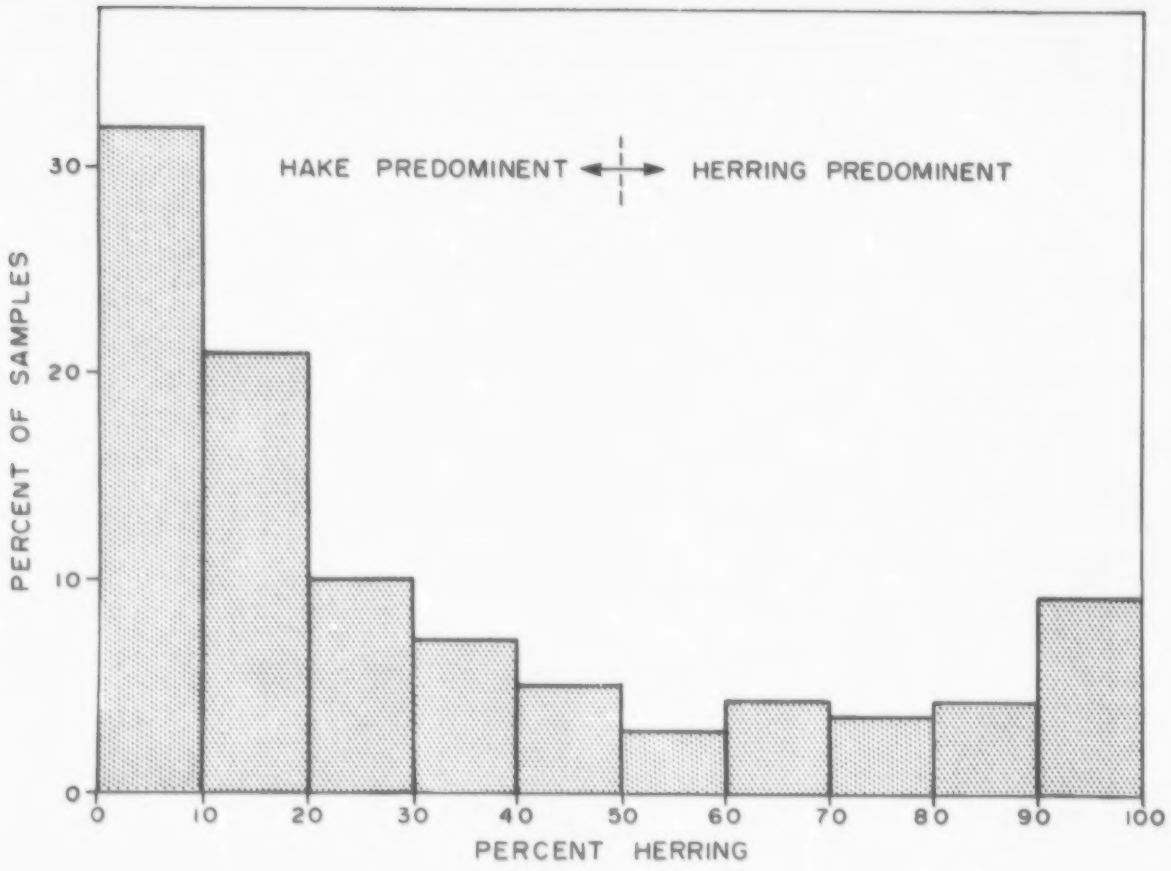


Figure 9. Relative volumetrically-weighted importance of herring and of hake (100 - percent herring) in those samples that contained both species. The estimates were obtained by averaging the three volumetric indices described in Appendix II.

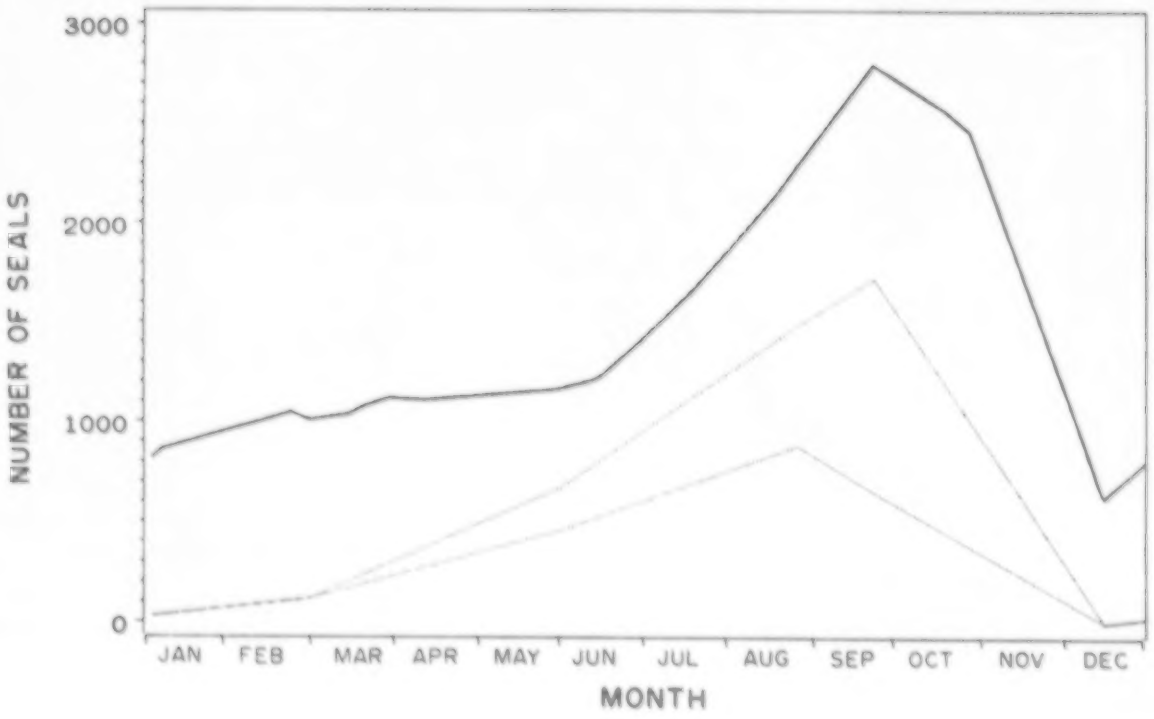
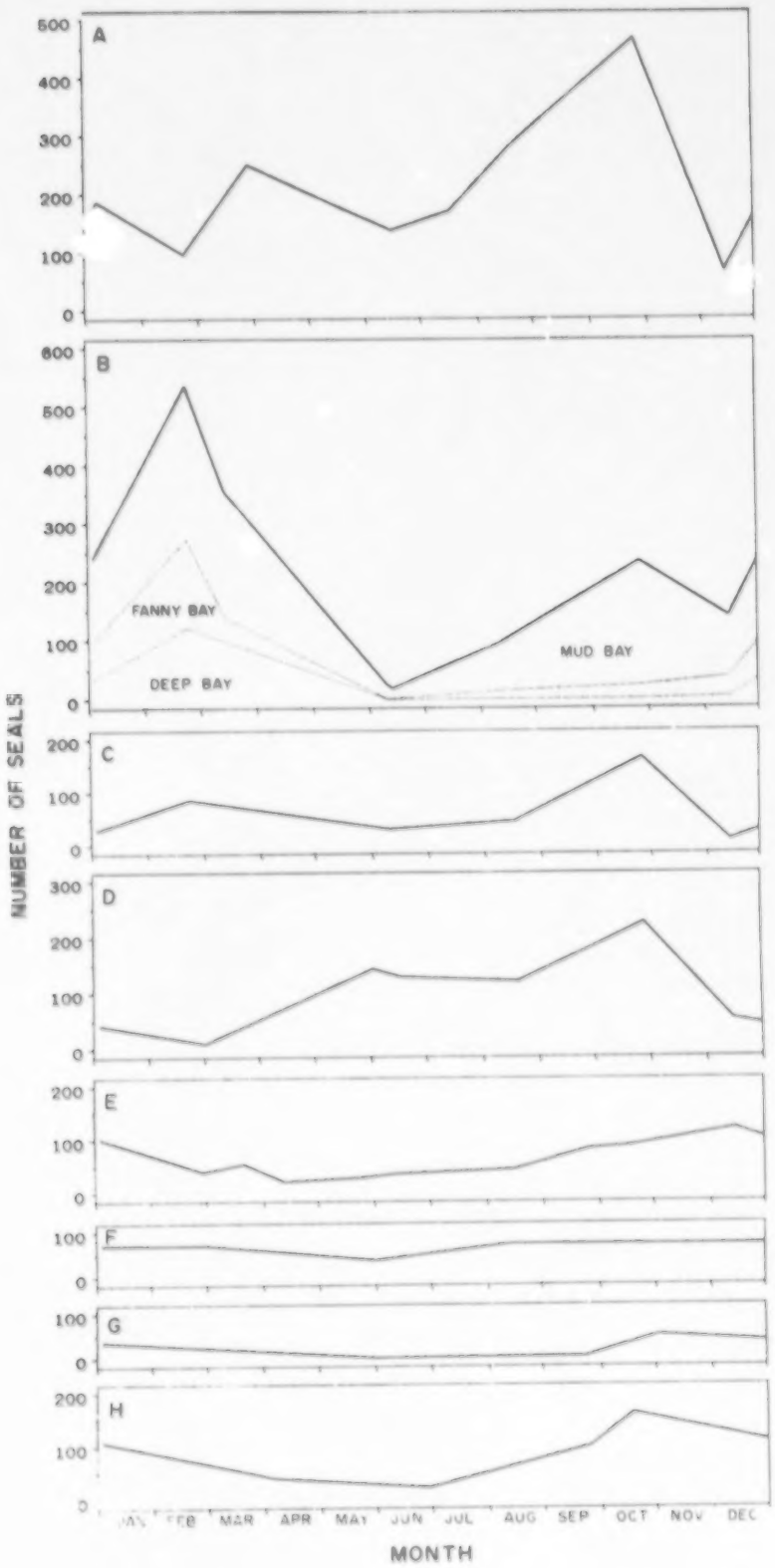


Figure 10. Seasonal changes in the total abundance of seals in estuaries. The dashed lines partition total abundance between Boundary Bay (bottom), the mouth of the Fraser River (middle) and all small estuaries combined (top; see Figure 11).

Figure 11. Seasonal changes in the abundance of seals in individual estuaries: a) Comox Harbour; b) Mud-Deep-Fanny Bays; c) Nanaimo River estuary; d) Shoal Islets; e) Cowichan Bay; f) Mill Bay; g) Squamish River estuary; and h) Port Moody. Replicated counts within months were averaged and plotted at the mean date of the counts. Abundance in Boundary Bay and the Fraser River are shown in Figure 10.


A
B
C
D
E
F
G
H
FANNY BAY
DEEP BAY
MUD BAY
NUMBER OF SEALS
MONTH
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

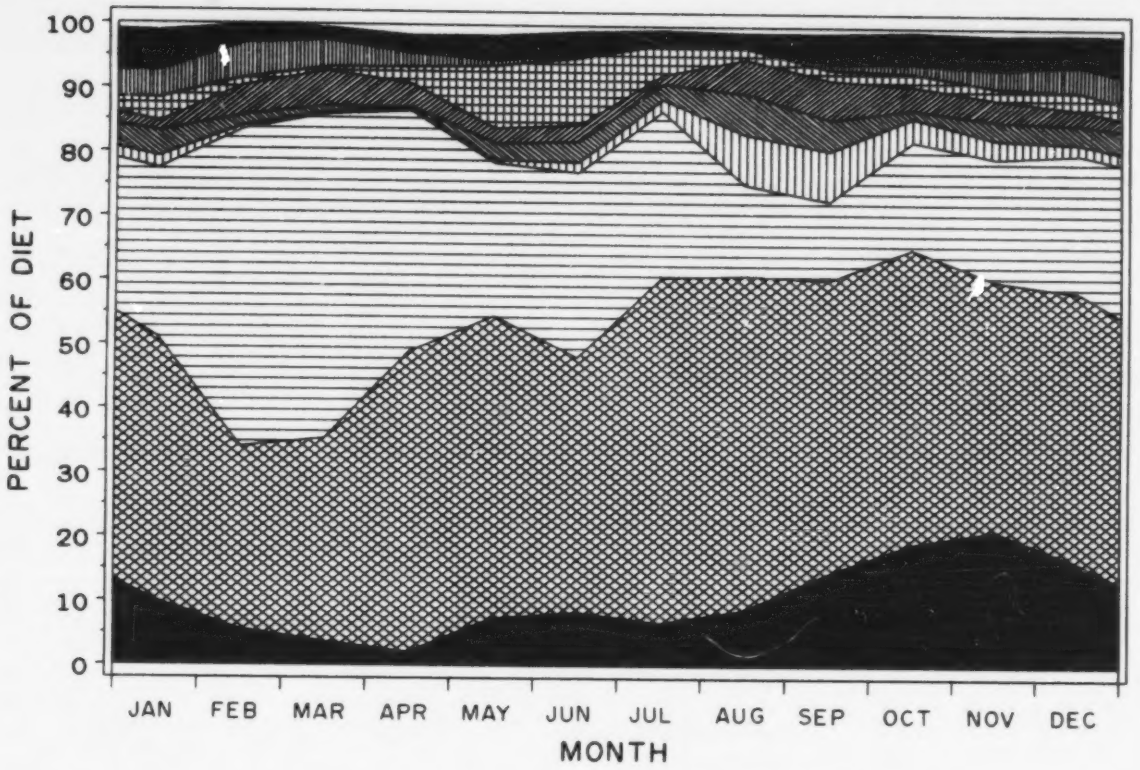


Figure 12. Seasonal changes in diet composition for all estuaries combined. Patterns used to denote prey are defined in Table 3.

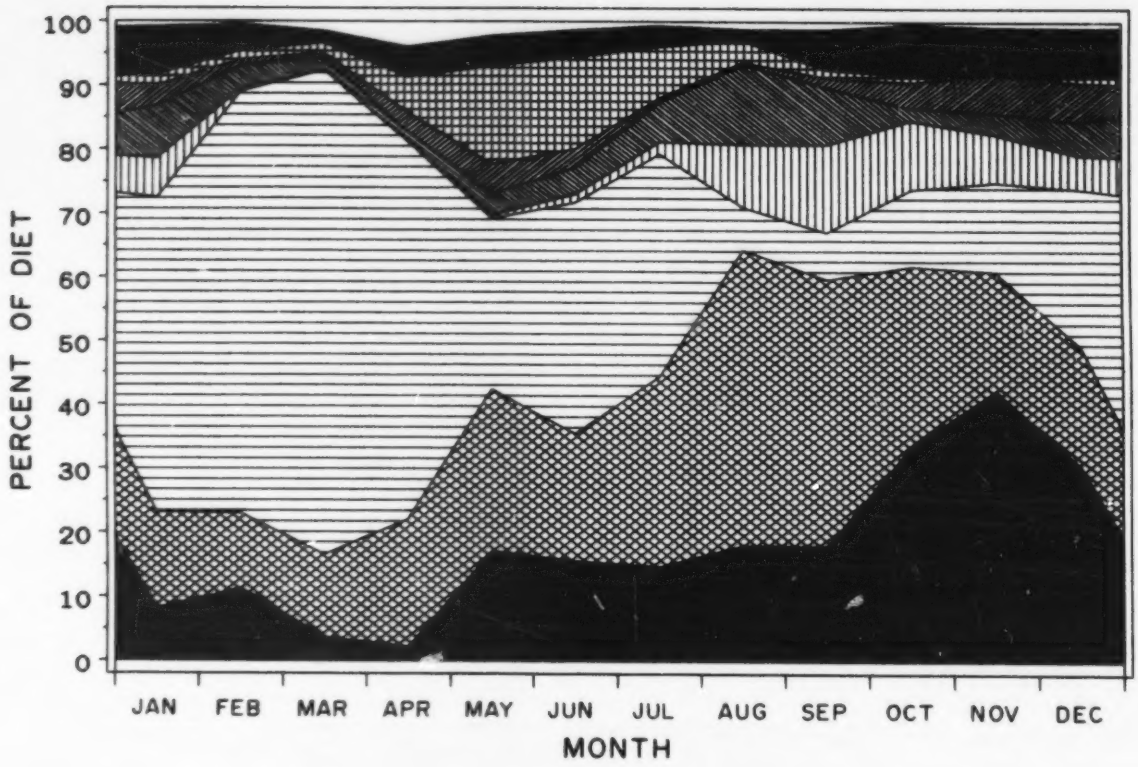


Figure 13. Seasonal changes in diet composition in Comox Harbour. Patterns used to denote prey are defined in Table 3.

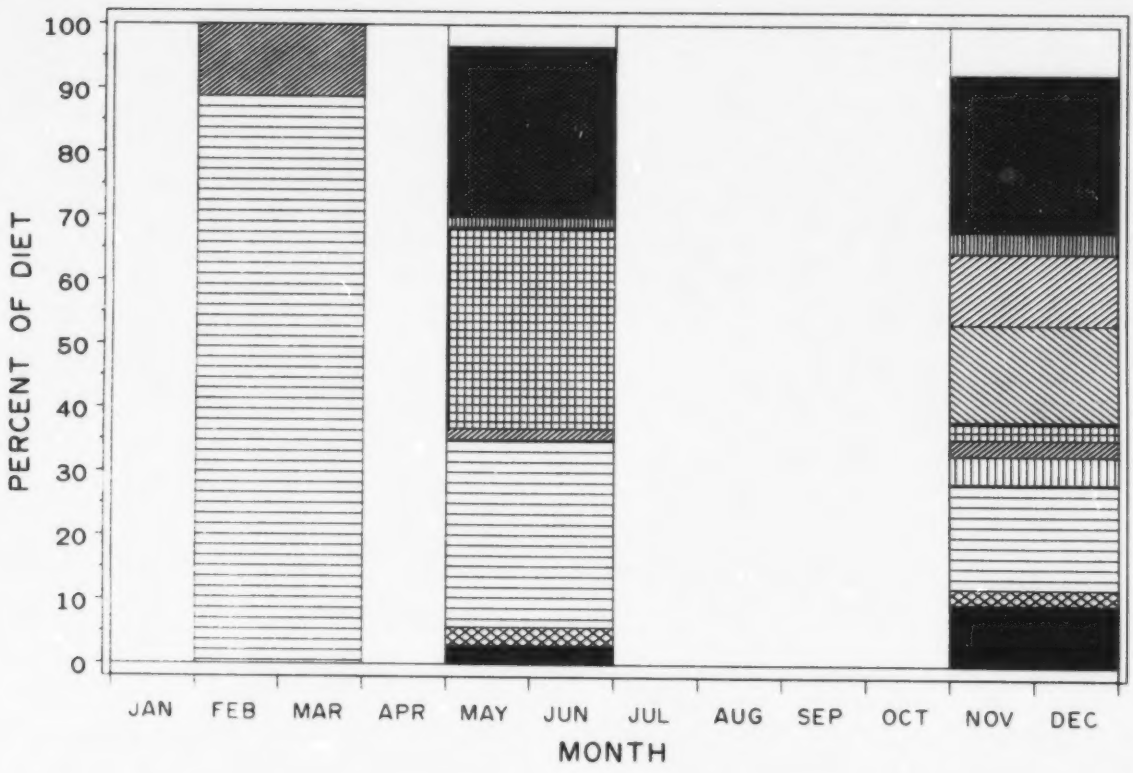


Figure 14. Seasonal changes in diet composition in Mud-Deep-Fanny Bays combined. Patterns used to denote prey are defined in Table 3.

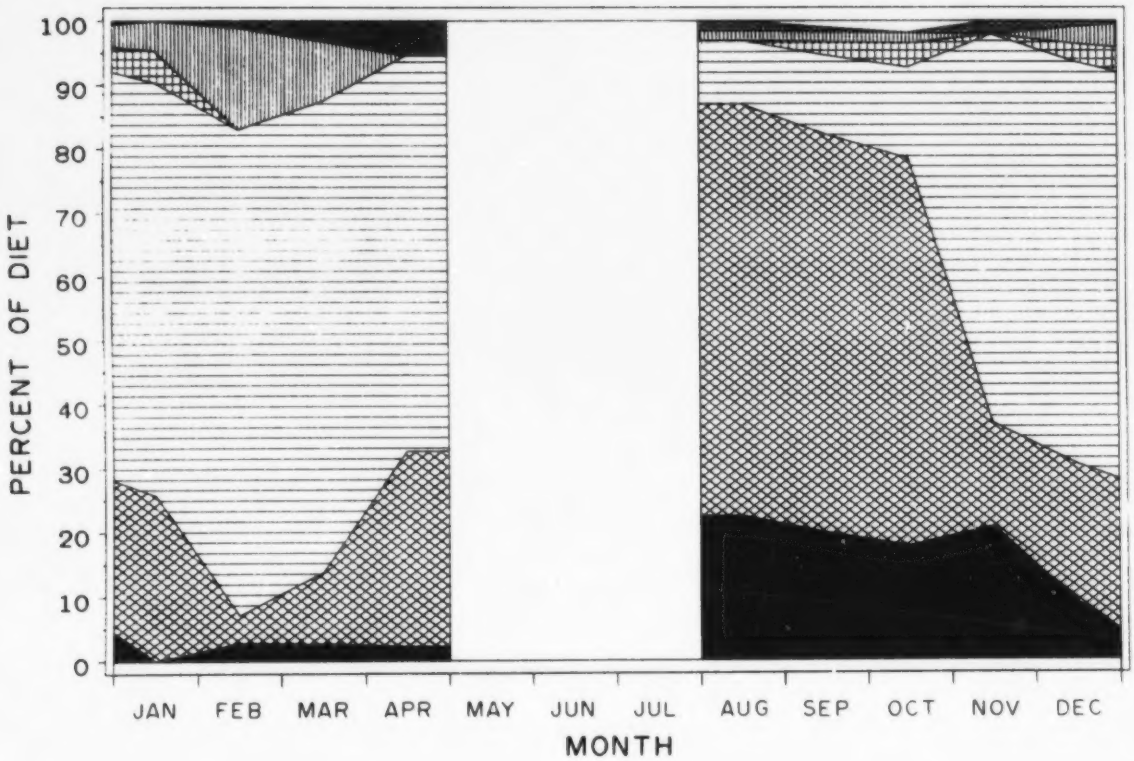


Figure 15. Seasonal changes in diet composition in the Nanaimo River estuary. Patterns used to denote prey are defined in Table 3.

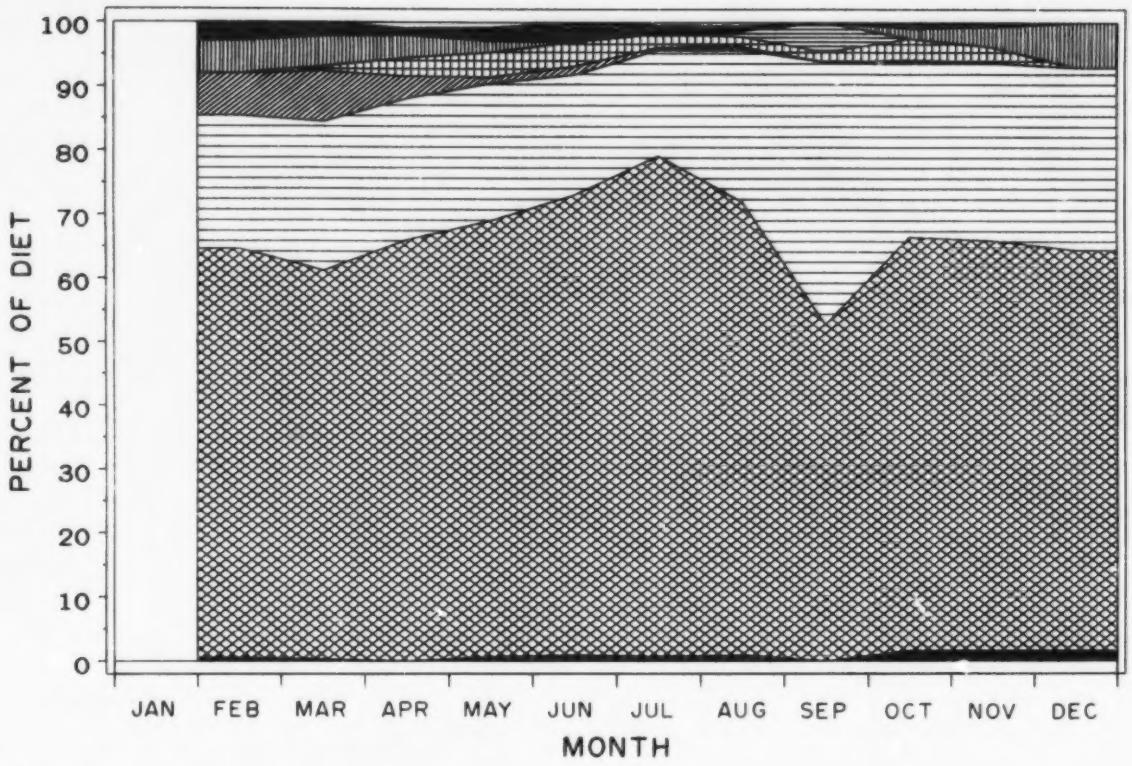


Figure 16. Seasonal changes in diet composition in the Shoal Islets. Patterns used to denote prey are defined in Table 3.

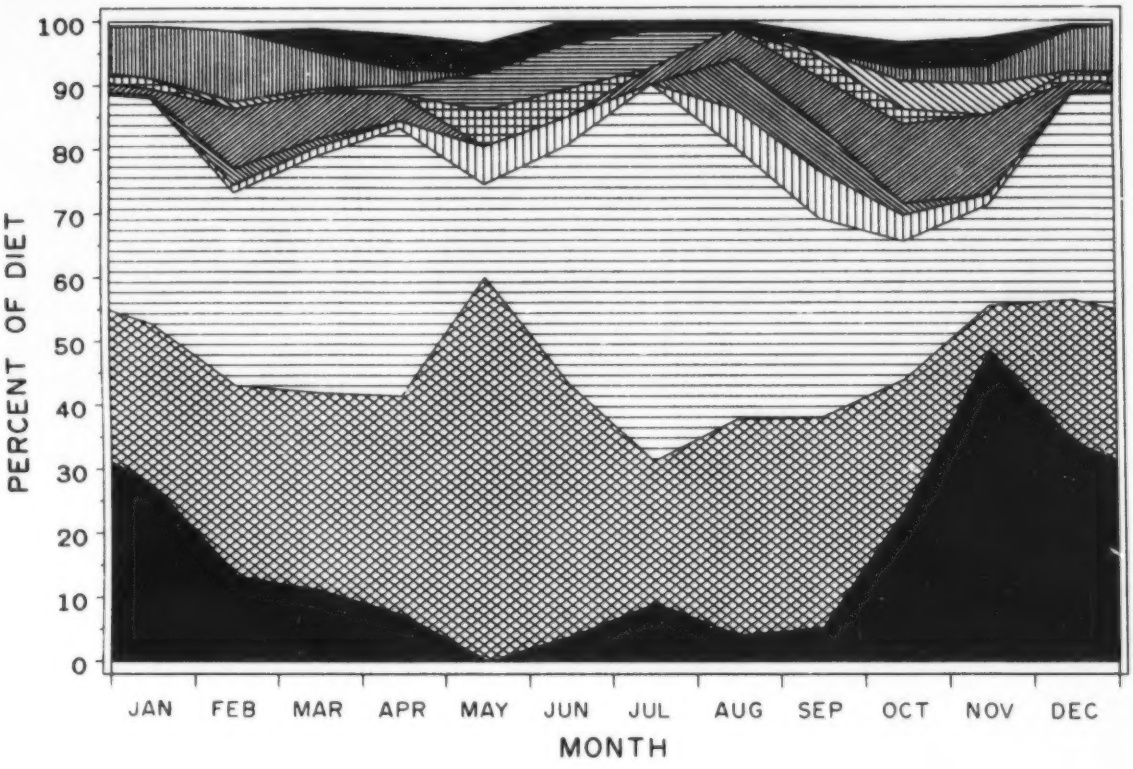


Figure 17. Seasonal changes in diet composition in Cowichan Bay. Patterns used to denote prey are defined in Table 3.

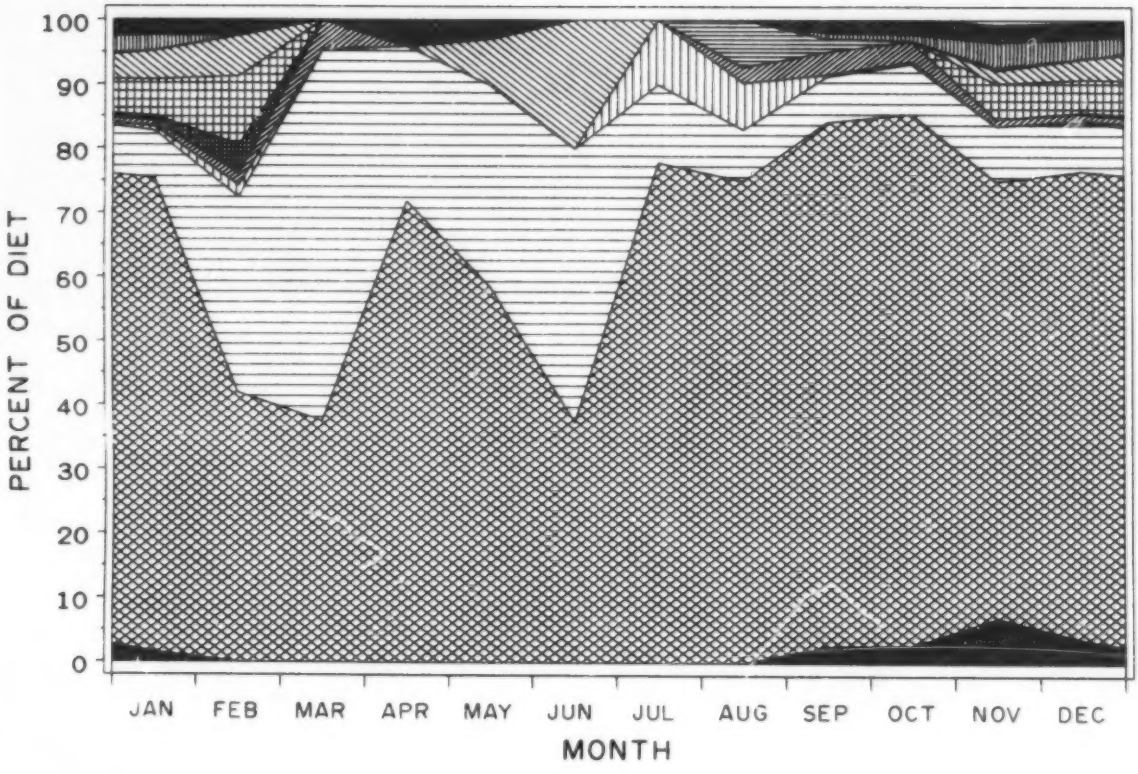


Figure 18. Seasonal changes in diet composition in Mill Bay. Patterns used to denote prey are defined in Table 3.

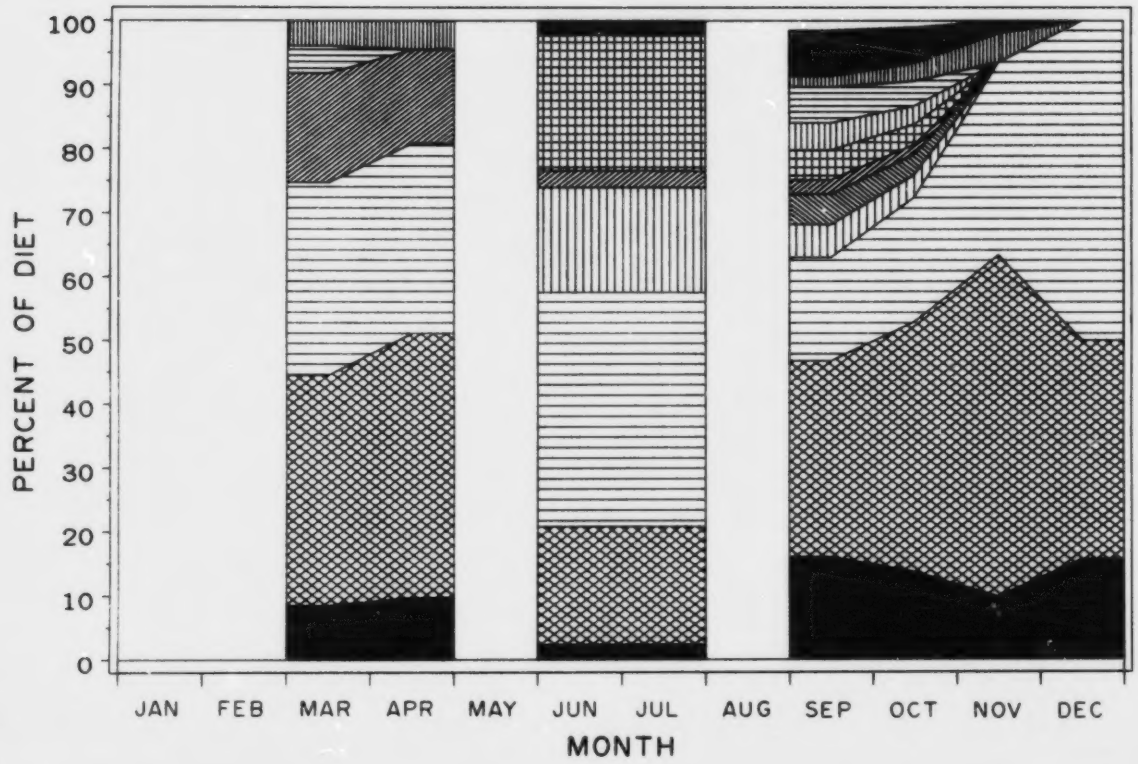


Figure 19. Seasonal changes in diet composition in Port Moody. Patterns used to denote prey are defined in Table 3.

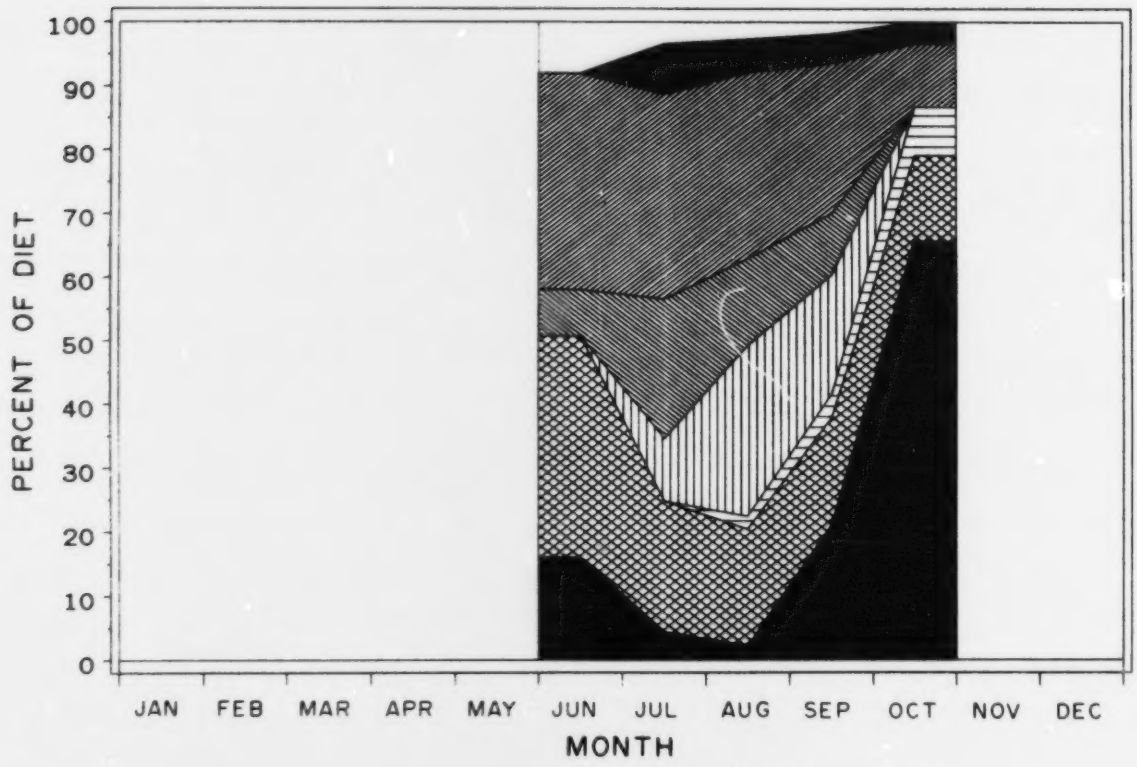


Figure 20. Seasonal changes in diet in Boundary Bay and the mouth of the Fraser River combined. Patterns used to denote prey are defined in Table 3.

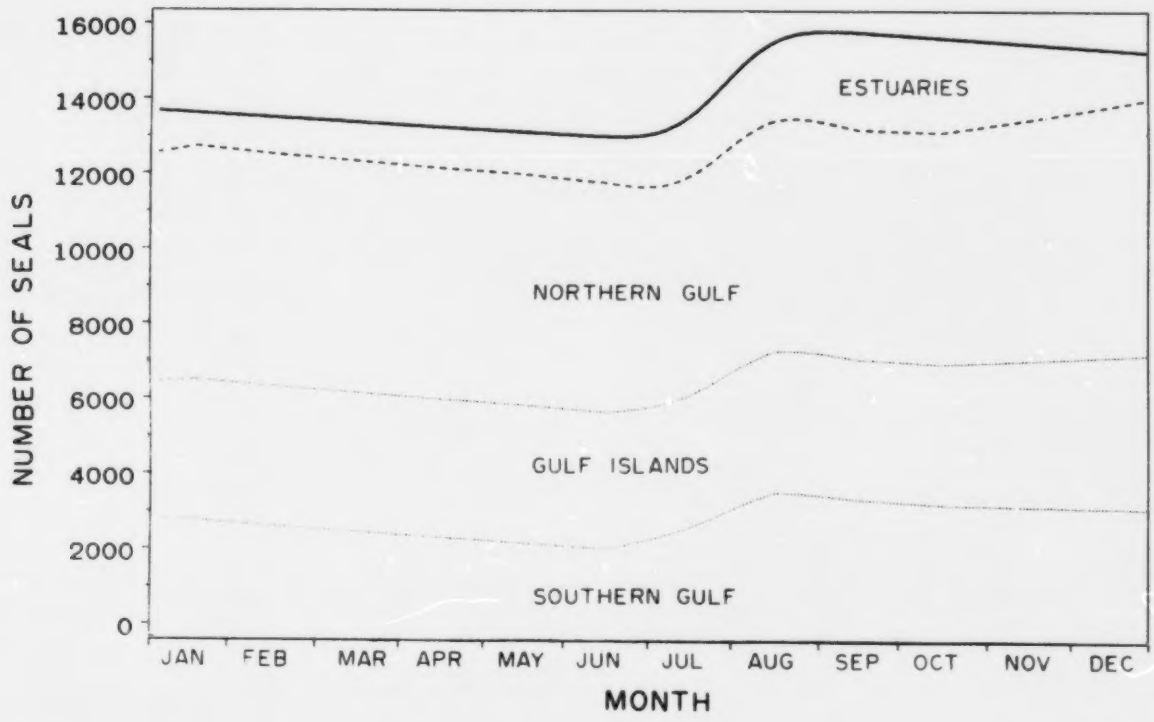


Figure 21. Seasonal fluctuations in size of the Strait of Georgia population during 1988 due to mortality and recruitment (solid line). The dashed line partitions the distribution between estuaries and non-estuaries and the dotted lines partition the latter between regions (as per Figure 2).

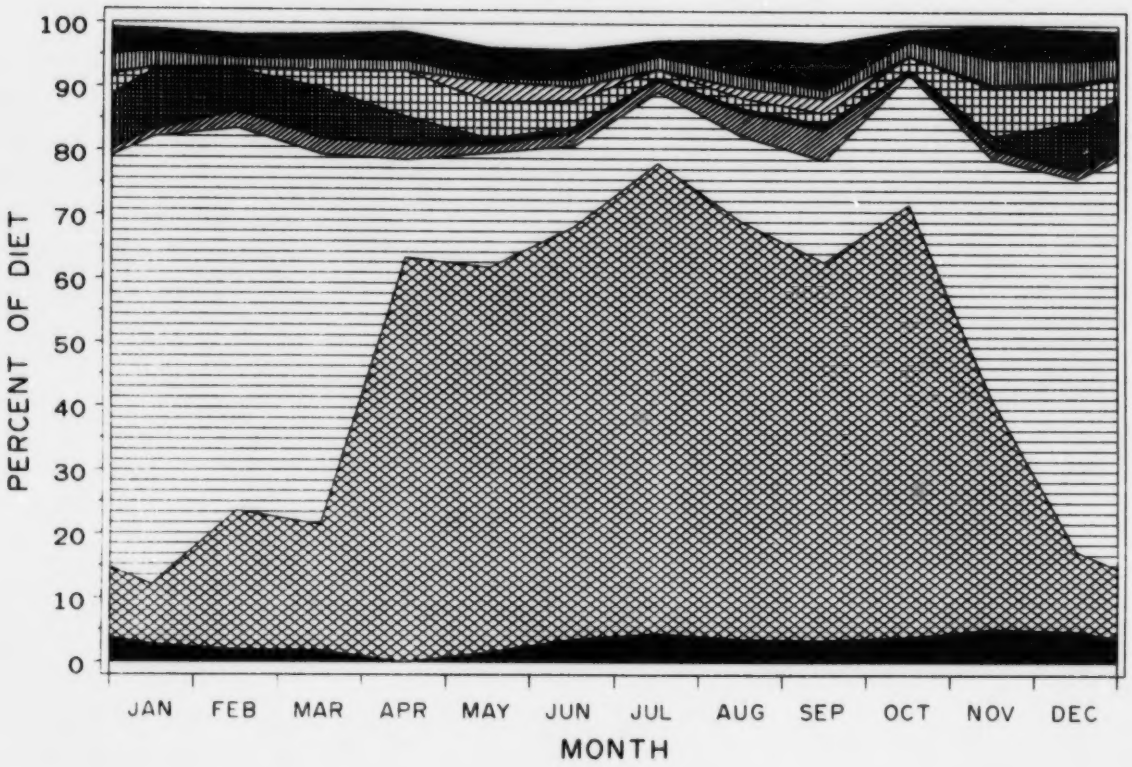


Figure 22. Seasonal changes in diet composition for all non-estuary sites in the Strait of Georgia combined. Patterns used to denote prey are defined in Table 3.

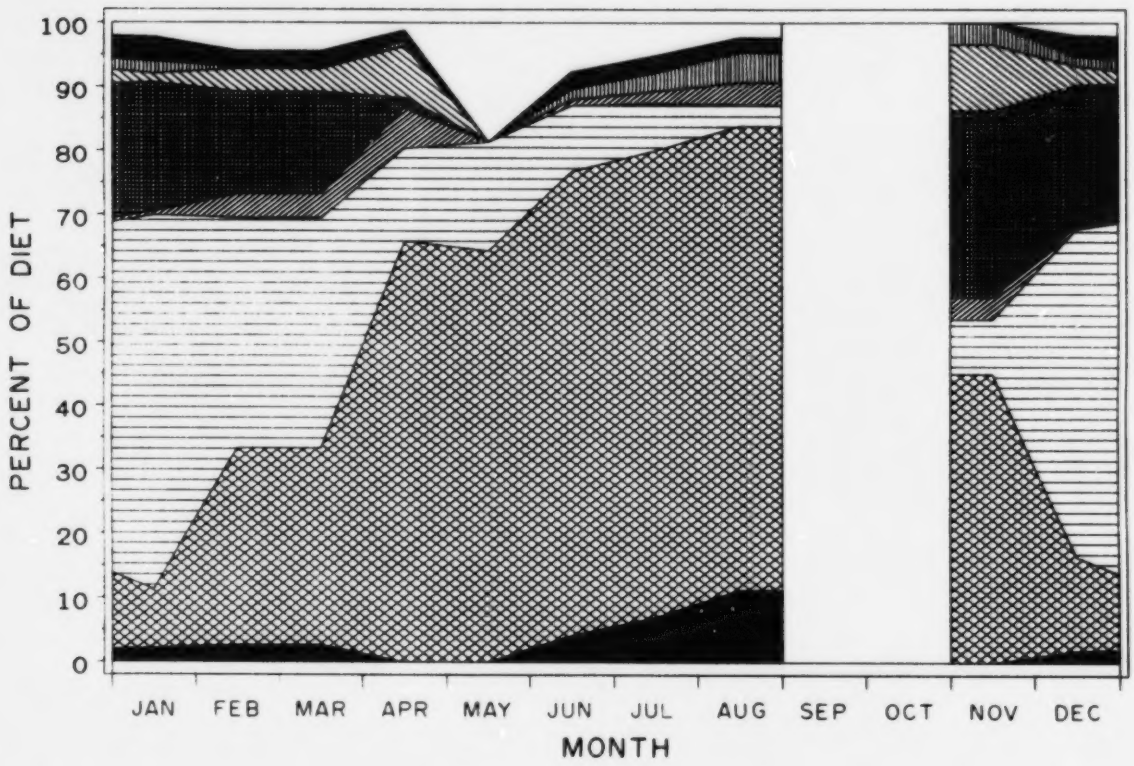


Figure 23. Seasonal changes in diet composition for all non-estuary sites in the Northern Gulf. Patterns used to denote prey are defined in Table 3.

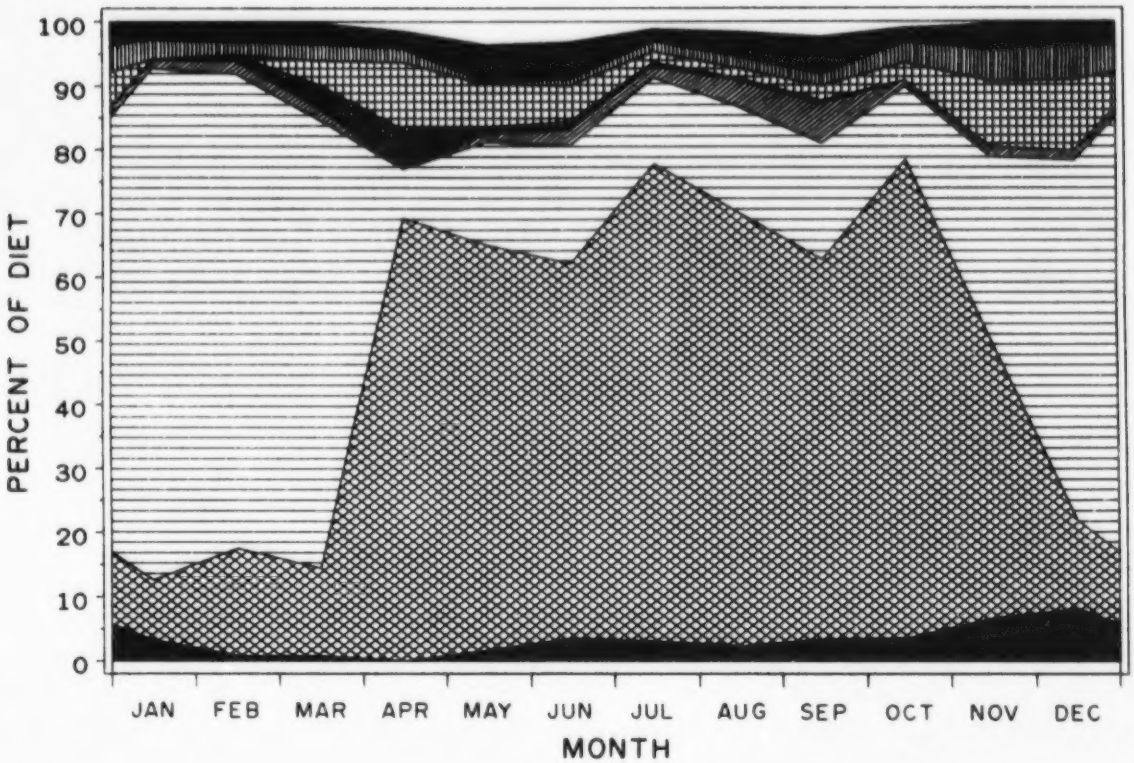


Figure 24. Seasonal changes in diet composition for all non-estuary sites in the Gulf Islands. Patterns used to denote prey are defined in Table 3.

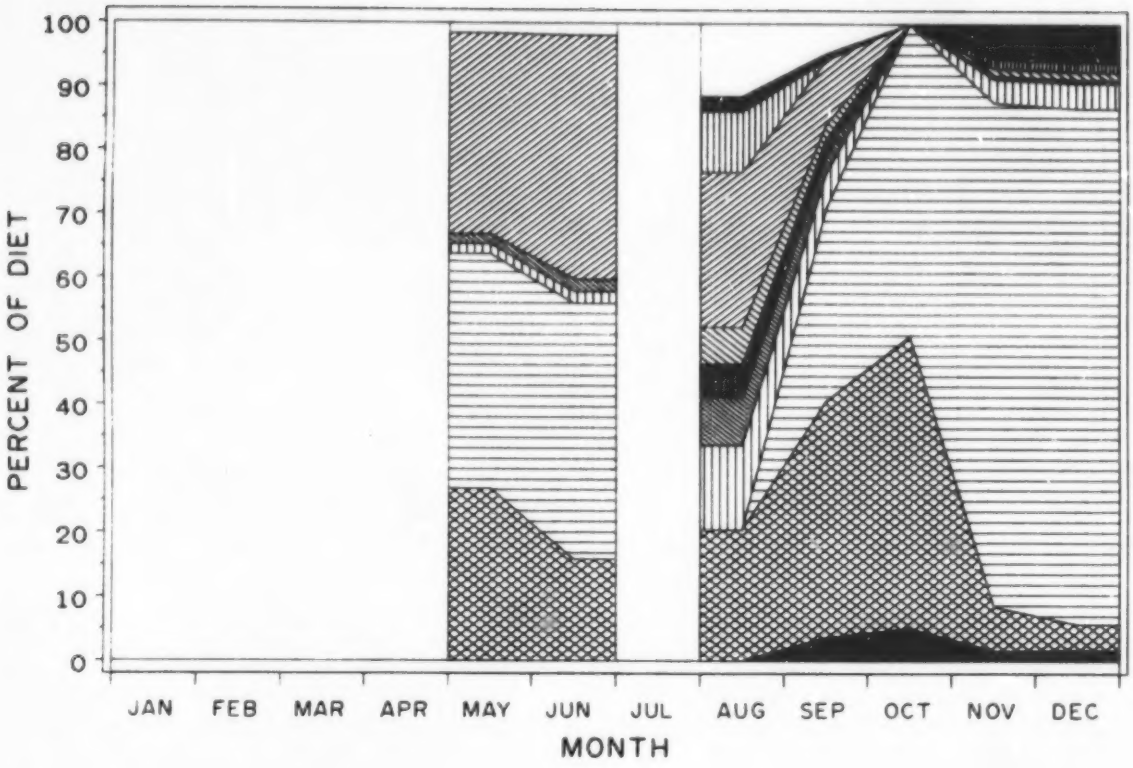


Figure 25. Seasonal changes in diet composition for all non-estuary sites in the Southern Gulf. Patterns used to denote prey are defined in Table 3.

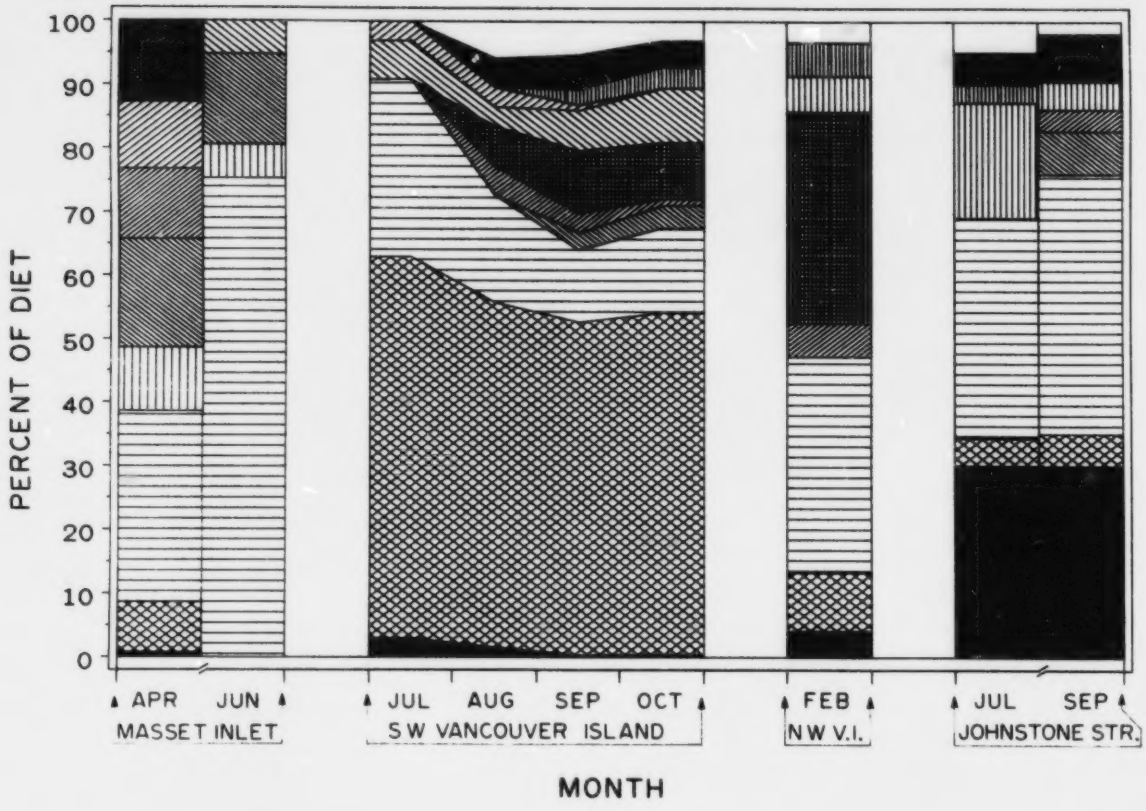


Figure 26. Diet composition at sites outside the Strait of Georgia. Note that diets for Masset Inlet and Johnstone Strait are not for consecutive months.

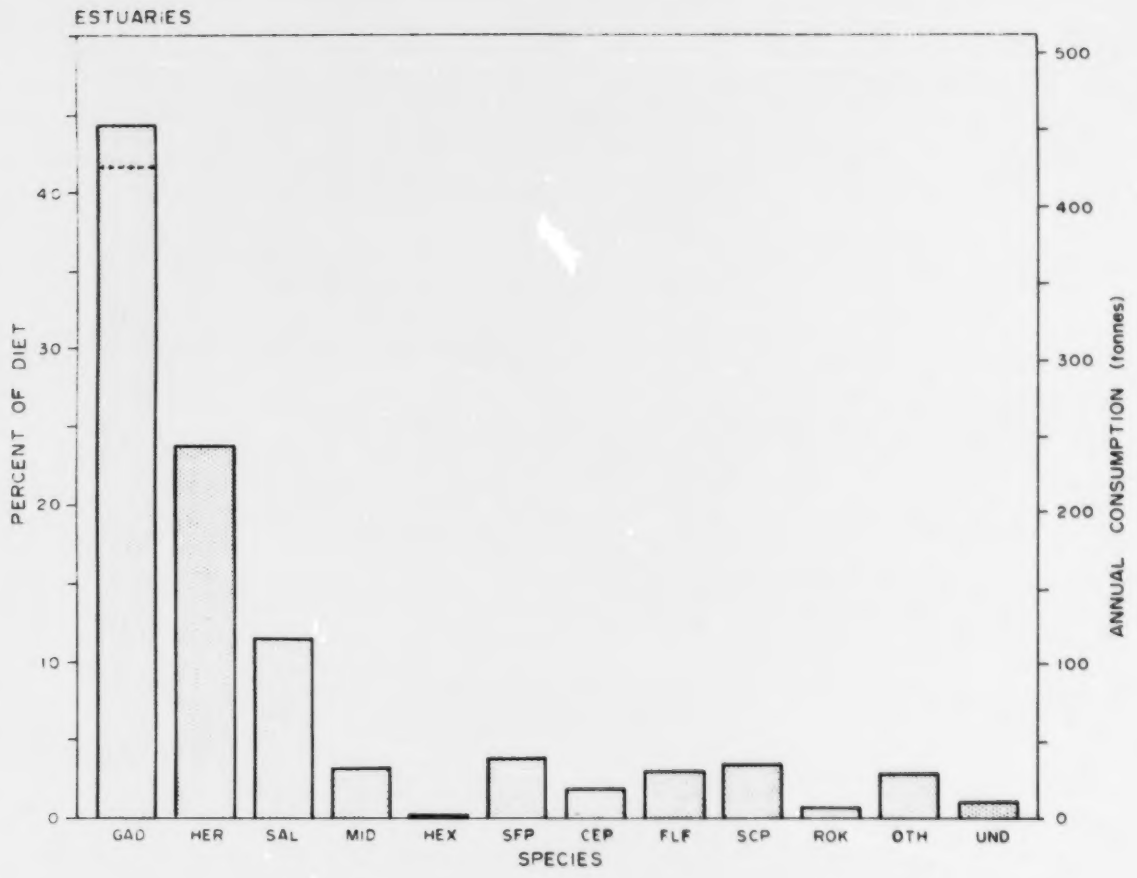


Figure 27a. Estimated absolute importance and annual consumption of prey in the Strait of Georgia within estuaries. The dashed lines partition gadoid consumption into hake (lower) and all other species (upper). Estimates are based on a low-level stratification (i.e. all estuaries pooled).

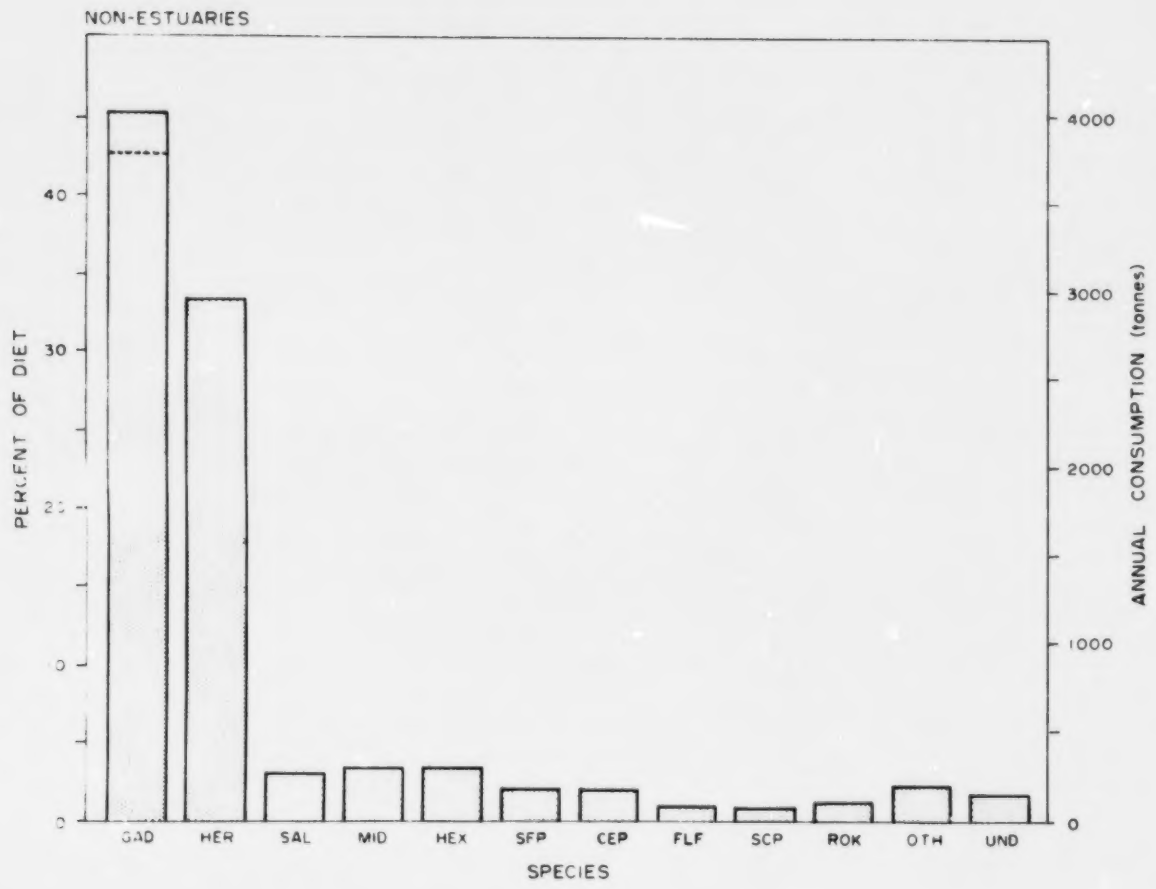


Figure 27b. Estimated absolute importance and annual consumption of prey in the Strait of Georgia outside estuaries. The dashed lines partition gadoid consumption into hake (lower) and all other species (upper). Estimates are based on a low-level stratification (i.e. all non-estuary sites pooled).

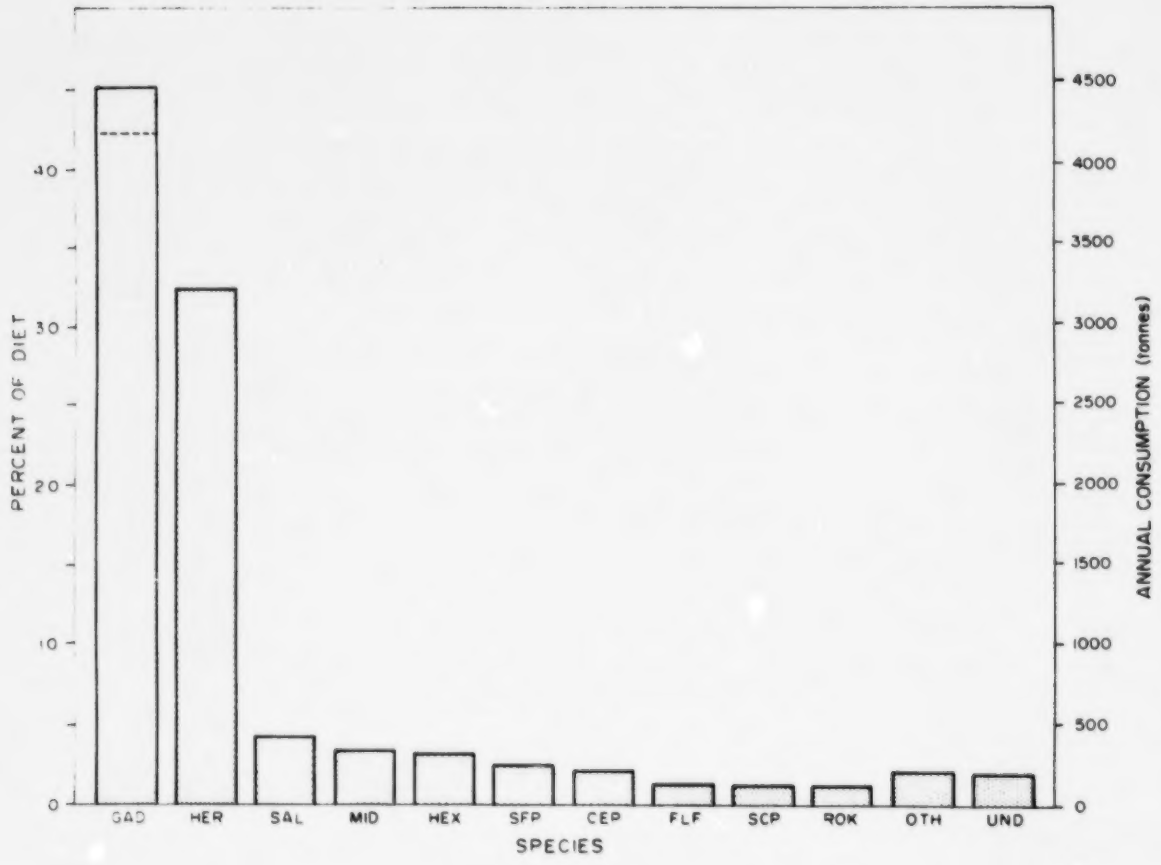


Figure 27c. Estimated absolute importance and annual consumption of prey in the total Strait of Georgia. The dashed lines partition gadoid consumption into hake (lower) and all other species (upper). Estimates are based on a low-level stratification (i.e. all estuaries pooled and all non-estuary sites pooled).

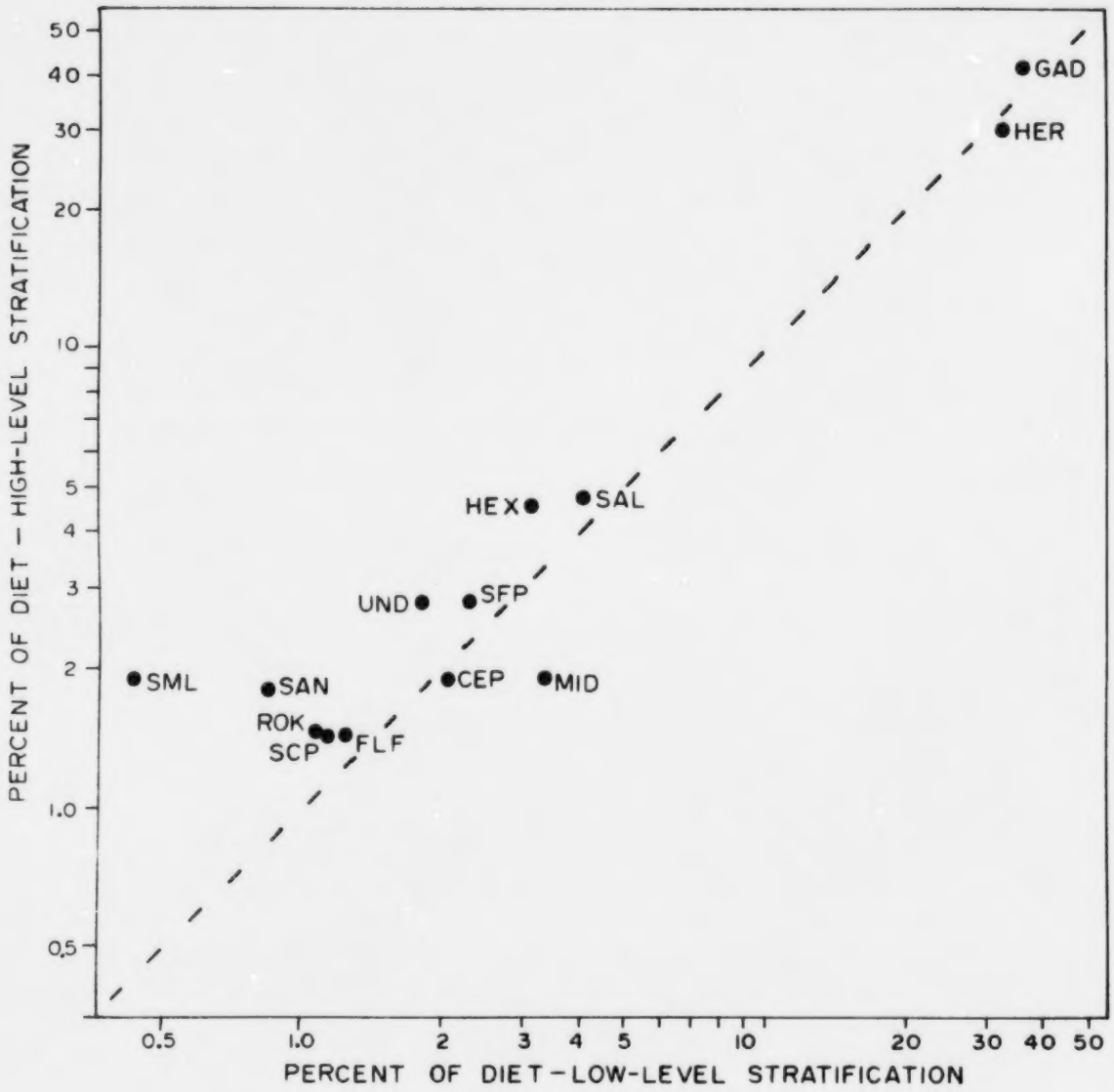


Figure 28. Comparison of the relative importance of important prey (>1% of diet) as indicated by the high- and low-level stratification schemes. The dashed line represents a 1:1 agreement line. Species codes are defined in Table 1. Data were too aggregated and fell too close to the agreement line (r^2=0.996) to show the same relationship on an arithmetic scale (i.e. in absolute terms).

APPENDIX I

Table A1. Summary of skeletal elements (and their codes) utilized to identify fish prey. Nomenclature generally follows that of Cannon (1987), Gregory (1933) and Starks (1901); and Norden (1961) for salmonids. As indices of the usefulness of each structure, we indicate: the total number of different prey species identified by each (SP); the total number of prey identifications in which each was present (ID); and the total numbers of each present in all samples (TN). A greater sign for the latter denotes that only the minimum number was recorded for some samples.

Code:	Structure:	SP:	ID:	TN:
	Cranium			
BAS	Basioccipital	25	385	1,289
BSP	Basisphenoid	1	5	5
CRA	Cranial bones (misc.)	31	922	>8,056
EPT	Epiotic	1	2	2
ETH	Ethmoid	1	1	1
EXO	Exoccipital	2	3	79
FRN	Frontal	6	11	75
PAR	Parasphenoid	8	25	188
PRF	Prefontal	15	60	259
PRO	Prootic	2	1,085	15,767
PTR	Pterotic	5	16	25
SPT	Sphenotic	2	33	56
VOM	Vomer	18	304	743
	Lateral skull			
ANG	Angular (retroarticular)	12	624	1,613
ART	Articular	20	537	1,903
CER	Ceratohyal	18	191	1,135
DEN	Dentary	19	114	701
EPI	Epihyal	17	591	1,772
HYH	Hypohyal	19	451	1,040
HYO	Hyomandibular	18	93	371
IOP	Interopercular	4	18	43
MAX	Maxilla	14	234	523
MET	Metapterygoid	2	6	7
MSP	Mesopterygoid	2	2	2
NAS	Nasal	1	1	2
OPE	Opercular	13	271	808
ORB	Orbital (misc.)	1	1	1
PAL	Palatine	13	54	71
POS	Pre-opercular spine	3	38	255
PRE	Pre-opercular	15	60	259

Table A1 (cont'd)

Code:	Structure:	SP:	ID:	TN:
	Lateral skull			
PRM	Premaxilla	20	158	440
PTG	Pterygoid	5	15	20
QUA	Quadrate	27	786	2,395
SMX	Supramaxilla	2	8	11
SOB	Suborbital	9	54	103
SOP	Subopercular	9	22	29
SYM	Symplectic	5	41	61
TRF	Tooth row fragment (sockets)	1	1	2
URO	Urohyal	11	82	179
	Branchial arch			
BRP	Branchial/pharyngeal (misc.)	19	181	422
BSB	Basibranchial	2	4	12
BSH	Basihyal	3	3	24
GRK	Gill raker/teeth	12	1,007	>2,247
HYB	Hypobranchial	4	290	620
IPH	Inferior pharyngeal	13	176	1,278
PHB	Pharyngeobranchial	9	59	132
SLG	Supralingual	2	13	29
SPH	Suprapharyngeal	5	69	735
	Appendicular elements			
ACT	Actinost (radial/pterygiophore)	4	20	30
CLE	Cleithrum	10	21	99
FIH	First interhaemal spine	1	8	17
FNR	Fin ray	4	22	87
HYC	Hypocorocoid	4	7	18
HYD	Hypercorocoid	8	23	48
IHS	Intrahaemal spine	1	3	6
MES	Mesocorocoid	1	7	7
PCL	Postcleithrum	4	31	78
PLS	Pelvic spine	1	2	4
PLV	Pelvis (Basipterygium)	10	37	179
PSC	Postcleithrum	2	4	4
PTM	Post-temporal	20	91	174
SCL	Supracleithrum	14	117	248
SCP	Scapula	3	3	3

Table A1 (cont'd)

Code:	Structure:	SP:	ID:	TN:
	Axial skeleton			
ATL	Atlas vertebrae	8	44	259
PTP	Pterygiophore (actinost)	3	15	54
PVE	Penultimate vertebrae	1	1	1
SPI	Spine	9	22	103
RAR	Rib/vertebrae articular	1	2	3
VEF	1st/2nd vertebrae	18	785	5,456
VEP	Vertebral process	2	3	3
VER	Vertebrae	45	3,850	>132,168
	Caudal skeletion			
CAU	Caudal (misc. hyperals/epurals)	3	8	14
CBP	Caudal bony plate (salmonids)	1	1	1
HYP	Hypural	7	28	62
UVE	Ultimate vertebrae	12	323	1,276
	Miscellaneous			
CRF	Cartilage fragment	1	1	6
EYE	Eye lens - size not recorded	1	51	474
EYL	Eye lens - large (4-6mm)	1	172	333
EYM	Eye lens - medium (2-4mm)	1	1,008	3,758
EYS	Eye lens - small (1-2mm)	1	1,221	9,679
EYT	Eye lens - tiny (<1mm)	1	544	>5,341
EYV	Eye lens - very large (>6mm)	1	4	4
FRA	Fragmant (miscellaneous)	6	28	>38
OTO	Otolith (saggitae)	38	2,140	14,518
OTS	Otolith (not saggitae)	2	9	21
ROE	Eggs	1	3	3
SCU	Scute	6	38	282
TEE	Teeth	24	1,289	>4,269
ZZZ	Unknown structure	2	4	5

APPENDIX II

Volumetric index for weighting hake and herring

Numerical analyses of hake and herring elements in samples containing both species indicated that elements of one species were generally more abundant than the other, which implied that one of the species had been consumed in greater numbers than the other. In most cases, hake elements were more prevalent than herring elements, which suggested that the former constituted the bulk of the meal and the latter was an incidental prey item. On average, herring elements were less abundant in the samples that also contained hake than in the samples comprised entirely of herring (Table A1), even though the former were usually larger in volume. On the other hand, hake elements were approximately equally abundant in samples that contained both species and in samples comprised entirely of hake (Table A1). The above trends were consistent among all the structures used to identify these prey species (Table A1). Thus, the assumption that both species had been consumed in equal quantities implicit to the split-sample frequency index appeared to be invalid.

To account for this bias, we derived a volumetric-weighting index based on the relative number of skeletal elements of each species present in samples containing both, relative to the number of elements in samples comprised exclusively of each species. Owing to the differences in the ratios of the various structures in whole prey, their recovery rates, and their identifiability, the various structures varied in their relative abundance. Thus, the first step in deriving the volumetric index involved scaling the structures to common units. We arbitrarily re-scaled all elements to units referred to as vertebrae-equivalents (*VE*s):

$$[A1] \quad VE_{HER,i} = \sum_{k=1}^{n} NSTR_{HER,ki} \cdot \left(\sum\sum_{i=k=1}^{Nn} NSTR'_{HER,ki} / \sum_{i=1}^{N} VER'_{HER,ki} \right)$$

and

$$[A2] \quad VE_{HAK,i} = \sum_{k=1}^{n} NSTR_{HAK,ki} \cdot \left(\sum\sum_{i=k=1}^{Nn} NSTR'_{HAK,ki} / \sum_{i=1}^{N} VER'_{HAK,i} \right)$$

where $NSTR_{ki}$ represents the number of the kth of n structures of the species in the ith of N samples, and $\Sigma\Sigma NSTR'_{ki}$ and $\Sigma VER'_{i}$ the total sum of the number of the kth structure and vertebrae respectively in all the samples comprised exclusively of that species. The number of *VE*s were calculated on the basis of only those structures that were routinely enumerated and which occurred in at least 20% of the samples that contained the species. These were ANG, EPI, HYB, HYH, OTO, VER and VOM for hake; and OTO, PRO, VEF and VER for herring (see Appendix I for codes). Note that since the *VE*s were based on the relative abundance of each

structure, the total number of elements could just as easily have been re-scaled into terms of any other structure (e.g. otolith-equivalents) with the exact same results. It should also be noted that, owing to the high degree of multi-collinearity between the abundance of the various structures in samples, the direct ratio re-scaling method (equations A1 and A2) was considered more appropriate than a multiple-regression (of the number of various structures on the number of vertebrae in samples) approach.

Three different approaches were used to calculate the volumetric-weighting index. In the first, the number of *VE*s in samples comprised exclusively of each of the two species was regressed on sample-volumes and the regressions subsequently used to predict the relative volumes of the sample affiliated with each species in samples containing both species. For both species, the intercepts of the regressions were not significantly different from zero ($P>0.20$), so both were forced through the origin. The relative proportion of their combined volume of each prey species in the *i*th sample [Pr(*HER*)and Pr(*HAK*)] were thus estimated by:

$$[A3] \quad Pr(HER)_i = \hat{VOL}_{HER} / (\hat{VOL}_{HER} + \hat{VOL}_{HAK})$$

$$[A4] \quad Pr(HAK)_i = 1-Pr(HER)_i$$

where $\hat{VOL}_{HER}$ and $\hat{VOL}_{HAK}$ represent the predicted volumes for each sample affiliated with herring and hake respectively based on the slopes of the regressions of *VE* on volume (0.086 for herring and 0.305 for hake). This approach would have been preferred had it not been for the small correlation coefficients ($r=0.675$ for hake and $r=0.611$ for herring) of the predictive regressions.

In the second approach, we ignored sample-volumes and calculated the index on the basis of the relative mean number of *VE*s in all samples comprised exclusively of each of the two species:

$$[A5] \quad Pr(HER)_i = \frac{(VE_{HER_i}/\overline{VE}_{HER})}{(VE_{HER_i}/\overline{VE}_{HER})+(VE_{HAK_i}/\overline{VE}_{HAK})}$$

$$[A6] \quad Pr(HAK)_i = 1-Pr(HER)_i$$

where $\overline{VE}_{HER}$ and $\overline{VE}_{HAK}$ represent the mean number of *VE*s in samples comprised exclusively of each species (278.1 for herring and 205.2 for hake). This approach would have been the most appropriate if the difference in the mean volumes of samples containing only herring ($\bar{x}$=51.9 ml) and only hake ($\bar{x}$=95.9 ml) were due to differences in the digestibility of the two species (i.e. hake samples were larger due, say, to a higher ash content, which might be expected given the lower caloric value of this prey - see Olesiuk in prep.).

In the third approach, we calculated the index on the basis of the

relative to mean number of *VE*s per unit volume in all samples comprised exclusively of each of the two species:

$$[A7]\quad Pr(HER)_i = \frac{(VE_{HER\,i}/\overline{VE}_{HER}\cdot ml^{-1})}{(VE_{HER\,i}/\overline{VE}_{HER}\cdot ml^{-1})+(VE_{HAK\,i}/\overline{VE}_{HAK}\cdot ml^{-1})}$$

$$[A8]\quad Pr(HAK)_i = 1-Pr(HER)_i$$

were $\overline{VE}_{HER}\cdot ml^{-1}$ and $\overline{VE}_{HAK}\cdot ml^{-1}$ represent the mean number of *VE*s per ml in samples comprised exclusively of each species (5.65 for herring and 2.66 for hake). This approach would have been the most appropriate if the difference in the mean volumes of samples containing only herring and only hake were due to differences in the proportion of the total samples comprised exclusively of either species that had been collected (i.e. a larger proportion of hake scats were collected, which might be expected as they tended to be less fluid than herring scats).

All three indices yielded similar results ($r^2>0.948$). The high degree of concordance between them can be explained by the fact that either hake or herring was usually much more predominant than the other in a sample, irrespective of how the index was calculated. The three approaches suggested that, on average, herring comprised a smaller proportion ($\bar{X}$=19-28%) of the total meal than did hake (72-81%). In view of the similarity of the three indices, and lack of definitive criteria for favouring one over the other two, their average values ($\bar{X}$=23% herring and 77% hake) were adopted for subsequent calculations (Figure 9). Moreover, additional calculations (PFO, unpubl. data) indicated that the index was robust to which of the skeletal elements were used to calculate the *VE*s, whether functional rather than predictive regressions were employed, etc.

Table A2. Mean number of representative herring and hake structures (number per ml) in samples comprised exclusively of either species (n=430 for herring and n=543 for hake) and in samples containing both species (n=794).

	Herring Structures		Ratio
Structure:	Herring only:	Herring and Hake:	Both/Herring:
ART	1.20 (0.023)	0.35 (0.003)	0.29 (0.15)
EPI	0.64 (0.012)	0.20 (0.002)	0.31 (0.16)
MAX	0.37 (0.007)	0.07 (0.001)	0.19 (0.10)
OPE	0.89 (0.017)	0.12 (0.001)	0.13 (0.07)
OTO	4.02 (0.077)	1.47 (0.014)	0.37 (0.19)
PRO	16.43 (0.317)	5.36 (0.051)	0.33 (0.17)
QUA	0.38 (0.007)	0.24 (0.002)	0.63 (0.32)
UVE	1.33 (0.026)	0.35 (0.003)	0.26 (0.13)
VEF	4.51 (0.087)	2.23 (0.021)	0.49 (0.25)
VER	62.89 (1.212)	25.09 (0.242)	0.40 (0.20)
Mean	- -	- -	0.34 (0.17)

	Hake Structures		Ratio
Structure:	Hake only:	Herring and Hake:	Both/Hake:
ANG	0.96 (0.010)	1.02 (0.010)	1.06 (0.98)
ART	0.39 (0.004)	0.50 (0.005)	1.28 (1.18)
BAS	0.51 (0.005)	0.57 (0.005)	1.14 (1.05)
EPI	0.63 (0.007)	0.55 (0.005)	0.87 (0.80)
HYB	0.37 (0.004)	0.43 (0.004)	1.16 (1.07)
HYH	0.52 (0.005)	0.61 (0.006)	1.17 (1.08)
OTO	2.61 (0.027)	2.53 (0.024)	0.97 (0.90)
QUA	0.68 (0.007)	0.88 (0.008)	1.29 (1.19)
VER	21.57 (0.225)	24.52 (0.236)	1.14 (1.05)
VOM	0.40 (0.004)	0.39 (0.004)	0.98 (0.91)
Mean	- -	- -	1.11 (1.02)

APPENDIX III

Salmonid escapement data

Table A3. Estimated mean stock size (# of fish), individual fish weight (kg), total stock biomass (mt), and timing of spawning of salmonids for each estuary in the Strait of Georgia and the entire Strait of Georgia.

Estuary[1]:	Species[2]:	Mean # fish[3]:	Mean ind. wt. (kg)[4]:	Mean run size (mt):	Timing of run[5] Start:	Peak:	End:
Comox Harbour	Sockeye	30	2.7	0.08	-	-	-
	Coho	17,390	2.7	46.95	E Oct	M Nov	L Jan
	Pink	12,490	2.3	28.73	L Oct	M Nov	L Dec
	Chum	61,680	4.6	283.73	M Sep	E Oct	L Dec
	Chinook	970	6.7	6.50	E Oct	M Oct	E Nov
	Steelhead	900	3.4	3.06	peaks in Jan-Apr and Aug-Oct		
	Cutthroat	850	0.4	0.34	in estuary during Jun-Sep		
	Total	-	-	369.39			
Deep-Mud-Fanny Bays	Coho	1,080	2.7	2.92	L Oct	L Nov	L Jan
	Pink	520	2.3	1.20	-	-	-
	Chum	7,720	4.6	35.51	E Oct	L Nov	L Dec
	Steelhead	130	3.6	0.47	Jan through Apr		
	Cutthroat	600	0.4	0.24	in estuary during Jun-Sep		
	Total	-	-	40.33			
Nanaimo River	Coho	3,180	2.7	8.59	E Oct	M Nov	M Jan
	Pink	10	2.3	0.02	M Sep	L Sep	L Sep
	Chum	48,000	4.6	220.80	E Oct	E Nov	M Dec
	Chinook	1,530	6.7	10.25	L Aug	L Sep	M Nov
	Steelhead	1,000	3.6	3.60	Feb through Apr		
	Cutthroat	200	0.4	0.04	in estuary during Jun-Sep		
	Total	-	-	243.30			
Shoal Islets	Coho	1,140	2.7	3.08	L Oct	L Nov	M Jan
	Chum	25,280	4.6	116.29	L Sep	E Nov	L Dec
	Chinook	470	6.7	3.15	M Sep	E Oct	M Nov
	Steelhead	230	3.4	0.78	peaks in Mar-May and Jun-Aug		
	Cutthroat	150	0.4	0.06	in estuary during Jun-Sep		
	Total	-	-	123.36			
Cowichan Bay	Coho	23,400	2.7	63.18	L Oct	L Nov	E Jan
	Chum	98,100	4.6	451.26	E Nov	E Dec	M Jan
	Chinook	4,530	6.7	30.35	E Oct	L Oct	M Nov
	Steelhead	2,750	3.6	9.90	Dec through Apr		
	Cutthroat	250	0.4	0.10	in estuary during Jun-Sep		
	Total			554.79			
Mill Bay	Coho	80	2.7	0.22	-	-	-
Squamish River	Sockeye	80	2.7	0.22	-	-	-
	Coho	11,230	2.7	30.32	E Sep	M Oct	L Jan
	Pink	3,290	2.3	7.57	L Aug	M Sep	L Oct
	Chum	139,340	4.6	640.96	E Oct	L Nov	M Jan
	Chinook	2,410	6.7	16.15	E Jun	M Aug	M Oct
	Steelhead	2,200	4.5	9.90	E Feb	L Mar	L May
	Cutthroat	+	0.4	?	in estuary during Jun-Sep		
	Dolly Varden	+	0.5	?	in estuary during Jun-Aug		
	Total			705.12			

Table A3 (cont'd)

Estuary[1]:	Species[2]:	Mean # fish[3]:	Mean ind. wt. (kg)[4]:	Mean run size (mt):	Timing of run[5] Start:	Peak:	End:
Port Moody	Coho	1,030	2.7	2.78	-	-	-
	Chum	630	4.6	2.90	-	-	-
	Cutthroat	+	0.4	?	in estuary during		Jun-Sep
	Total			5.68			
Boundary Bay	Coho	2,010	2.7	5.43	L Oct	M Nov	L Dec
	Steelhead	220	3.2	0.70	E Dec	E Mar	L Apr
	Cutthroat	+	0.4	?	in estuary during		Jun-Sep
	Dolly Varden	+	0.5	?	in estuary during		Jun-Aug
	Total		-	6.13			
Fraser River	Sockeye	1,813,430	2.7	4,896.26	L Jun	Jul-Sep	M Oct
	Coho	55,400	2.7	149.58	E Sep	E Oct	L Nov
	Pink	872,090	2.3	2,005.81	E Sep	L Sep	M Oct
	Chum	406,540	4.6	1,870.08	E Oct	M Nov	L Dec
	Chinook	86,250	6.7	577.88	E Apr	Jun-Sep	E Oct
	Steelhead	22,500	4.5	101.25	E Sep	Oct+Jan	L Jun
	Cutthroat	+	0.4	?	in estuary during		Jun-Sep
	Dolly Varden	+	0.5	?	in estuary during		Jun-Aug
	Total	-	-	9,600.86			
Entire Strait of Georgia	Sockeye	1,939,190	2.7	5,235.81			
	Coho	190,590	2.7	514.59			
	Pink	912,050	2.3	2,097.72			
	Chum	1,163,360	4.6	5,351.47			
	Chinook	104,910	6.7	702.90			
	Total	-	-	13,902.49			

Footnotes:

[1]Escapement for all known spawning systems entering each estuary and their tributaries:

Comox Harbour: Millard Creek, Puntledge River, Trent River, Tsolum River, Brooklyn Creek and Roy Creek.
Deep-Mud-Fanny Bays: Chef Creek, Cook Creek, Cowie Creek, McNaughton Creek, Rosewall Creek, Tsable River, Waterloo Creek and Wilfred Creek.
Nanaimo River: Nanaimo River, Departure Creek, Chase River and Beck Creek.
Shoal Islets: Chemainus River and Bonsall Creek.
Cowichan Bay: Cowichan River and Koksilah River.
Mill Bay: Shawnigan Creek (including Hollings Creek).
Boundary Bay: Nicomekl River and Serpentine River.
Port Moody: Noons Creek, Schoolhouse Creek, Sutterbrook Creek and Musum Creek.
Fraser River: Fraser River and all tributaries.
Squamish River: Squamish River and all tributaries.

[2]Species:

a) Salmon
Sockeye (Oncorhynchus nerka)
Coho (Oncorhynchus kisutch)
Pink (Oncorhynchus gorbuscha)
Chum (Oncorhynchus keta)
Chinook (Onchorhynchus tshawytscha)

b) Trout
Steelhead (Salmo gairdneri)
Cutthroat (Salmo clarki)
Dolly Varden (Salvelinus malma)

[3]Number of fish:

a) Salmon: Mean annual escapement for spawning years 1978/79 to 1987/88 as indicated by the Salmon Escapement Database (G. Hudson, Pacific Biological Station, Nanaimo, B.C; pers. comm. 22 September 1989). Except data for Port Moody are for the years 1986-88 (R. McVicar, SEP volunteer, Port Moody, pers. comm.).

b) Trout: approximate mean numbers during 1984-88 (C. Wightman, Ministry of Environment and Parks, Fish and Wildlife Branch, 2569 Kenworth Road, Nanaimo, British Columbia; pers. comm. 22 September 1989; and P. Caverhill, Ministry of Environment and Parks, Fish and Wildlife Branch, 10334 152 A Str., Surrey, British Columbia; pers. comm. 22 September 1989).

[4]Mean weight of fish:

a) Salmon: derived from British Columbia commercial catch statistics. Salmon. 1987. Department of Fisheries and Oceans, Pacific Region, Vancouver, British Columbia. Weights are whole weights from seine catches just prior to the time that each salmon species enters rivers to spawn for the South Coast District (Statistical Areas 11-27 pooled).

b) Trout: approximate whole weights of fish in rivers (C. Wightman and P. Caverhill; pers. comm. 22 September 1989).

[5]Timing of spawning:

a) Salmon: compiled from: 1) Fish Habitat Inventory and Information Program. 1988. Stream summary catalogue, Subdistrict #17, Nanaimo. Department of Fisheries and Oceans. Fisheries Branch, South Coast Division, Nanaimo, British Columbia. July 1988; 2) Fish Habitat Invertory and Information Program. 1988. Stream summary catalogue, Subdistrict #18, Duncan. Department of Fisheries and Oceans. Fisheries Branch, South Coast Division, Nanaimo, British Columbia. July 1988.; 3) Hancock, M.J. and D.E. Marshall. 1985. Catalogue of salmon streams and spawning escapements of Statistical Area 29, New Westminster Subdistrict. Can. Data Rept. Fish. Aquat. Sci. No. 495.; 4) Hancock, M.J. and D.E. Marshall. 1985. Catalogue of salmon streams and spawning escapements of Statistical Area 14, Comox-Parksville. Can. Data Rept, Fish. Aquat. Sci. No. 504.; 5) Hancock, M.J. and D.E. Marshall. 1986. Catalogue of salmon streams and spawning escapements of Statistical Area 28, Howe Sound-Burrard Inlet. Can. Data Rept. Fish. Aquat. Sci. No. 557.; and 6) R. Harrison, Depart-ment Fisheries and Oceans, Fisheries Branch, Fraser River/Northern British Columbia/Yukon Division, # 80, 6th Str., New Westminster, British Columbia, for migration times through the test fishery site at Albion on the Fraser River (50 km from river mouth; pers. comm. 22 September 1989).

b) Trout: times present in the river estuary (C. Wightman and P. Caverhill; pers. comm. 22 September 1989).